Conservation Assessment of Marbled Murrelets in British Columbia, A Review of the Biology, Populations, Habitat Associations and Conservation

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Pacific and Yukon Region 2002 Canadian Wildlife Service **Environmental Conservation Branch**



Technical Report Series Number 387



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CONSERVATION ASSESSMENT OF MARBLED MURRELETS IN BRITISH COLUMBIA: A REVIEW OF THE BIOLOGY, POPULATIONS, HABITAT ASSOCIATIONS, AND CONSERVATION

ALAN E. BURGER¹

Technical Report Series No. 387
Pacific and Yukon Region 2002
Canadian Wildlife Service

This series may be cited as:

Burger, A. E. 2002
Conservation assessment of Marbled Murrelets in British Columbia: a review of the biology, populations, habitat associations, and conservation Technical Report Series No. 387. Canadian Wildlife Service, Pacific and Yukon Region, British Columbia.

Issued under the Authority of the Minister of Environment Canadian Wildlife Service

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Issued under the Authority of the Minister of Environment Canadian Wildlife Service

Ministry of Supply and Services Canada 1993 Catalogue No. CW69-5/387E ISBN 0-662-32642-3 ISSN 0831-6481

Copies may be obtained from: Canadian Wildlife Service Pacific and Yukon Region 5421 Robertson Road, RR #1 Delta, British Columbia Canada V4K 3N2

Abstract

The Marbled Murrelet (Brachyramphus marmoratus; family Alcidae) is a Threatened species in British Columbia. This review, part of a Conservation Assessment undertaken by the Canadian Marbled Murrelet Recovery Team, focuses on the biology of the bird relevant to conservation and management. Within the species' range (Alaska through central California) there is no evidence of significant genetic differentiation. Demographic parameters are reviewed including: age of first breeding (likely 2-5 years); fecundity (0.17 to 0.22 female fledglings raised per female); adult survival (0.83-0.92 per annum); generation time (approx. 10 years); and proportion of population breeding (55-95%). Population models suggest that the rate of population growth (λ) ranges between 0.93 (declining population) to 1.02 (increasing population). Predation is the main cause of nest failure, and likely predators at nest sites include accipiters, owls, corvids (crows, ravens and jays), squirrels and other arboreal mammals. The current BC population was estimated to be 55,000-78,000 birds and the sparse long-term data suggest declines in parts of BC. Most nests were on large limbs (15-75 cm diameter) in large, old-growth conifer trees. Important features of suitable nest stands included: old-growth trees (typically >250 years old); large tree diameter; variation in tree size; variable canopy structure and/or gaps in the forest; epiphyte mats on branches; availability of potential platforms limbs; and low elevation. Most nests (84%) were below 1000 m, there was reduced stand occupancy with increasing elevation, and habitat quality (tree size, platform availability, epiphyte cover) tend to decrease with elevation. Slope and aspect showed variable effects: many nests were on steep slopes, and nest success in Desolation Sound increased with slope, but slope was not necessarily a good predictor of suitable habitat. Evidence on edge effects is contradictory: many nests were near forest edges; some nest predators were more common along edges, especially near human activities; one review showed reduced nest success near edges but a study in Desolation Sound showed no negative effects near edges and higher success near natural edges. Six studies using radar showed that watershed populations of murrelets were directly proportional to the areas of old-growth forest available, and some studies showed evidence of population declines with loss of habitat. Densities were higher on the west of Vancouver Island $(0.082 \pm 0.034 \text{ SD})$ birds per ha of suitable habitat) than on the BC mainland coast $(0.028 \pm 0.019 \text{ birds per ha})$. Marine habitats used by

murrelets varied considerably, but are usually shallow (<30 m) and in sheltered waters or within 0.5 km of exposed shores. Schooling fish and macro-zooplankton are the main prey eaten. Oil spills, gill-nets, purse-seining, sports angling, and aquaculture are threats at sea but their impacts in BC are poorly known. The effects on murrelets of chemical contaminants (e.g., organochlorines, dioxins, furans, PCBs, heavy metals) have not been studied. There is no evidence of negative effects from disease, parasitism, introduced species, or over-fishing of prey in BC.

Résumé

En Colombie-Britannique, le Guillemot marbré (Brachyramphus marmoratus, de la famille des Alcidae) est une espèce menacée. Cette étude, qui fait partie de l'évaluation de la conservation entreprise par l'Équipe canadienne de rétablissement du Guillemot marbré, porte principalement sur des aspects de la biologie de cet oiseau qui sont liés à la conservation et à la gestion de l'espèce. On n'observe aucune différentiation génétique à l'intérieur de l'aire de répartition (de l'Alaska jusqu'au centre de la Californie). Les paramètres démographiques suivants sont étudiés : l'âge au premier accouplement (probablement de 2 à 5 ans), la fécondité (0,17 à 0,22 oisillon femelle élevé par femelle), la survie des adultes (0,83-0,92 par année), la durée d'une génération (environ 10 ans) et la proportion de la population qui se reproduit (55-95 %). Selon des modèles de population, le taux de croissance de la population (λ) varie de 0,93 (population en déclin) à 1,02 (population en croissance). La prédation est la cause principale de l'échec de la nidification, et les prédateurs aux sites de nidification sont probablement les suivants : éperviers, chouettes et hiboux, corvidés (corneilles, corbeaux et geais), écureuils et autres mammifères arboricoles. En Colombie-Britannique, l'effectif actuel est évalué à 55 000-78 000 oiseaux, et les données éparses à long terme indiquent des déclins de population dans certains secteurs de la Colombie-Britannique. La plupart des nids étaient situés sur de grosses branches (diamètre de 15-75 cm) de grands conifères de vieux peuplements. Les principales caractéristiques des peuplements propices à la nidification sont les suivantes : arbres de vieux peuplements (souvent de plus de 250 ans), grand diamètre des arbres, variation de la taille des arbres, variation de la structure du couvert et/ou des ouvertures dans le couvert, tapis d'épiphytes sur les branches, présence de branches pouvant servir de plates-formes et faible altitude. La plupart des nids (84 %) se trouvent à moins de 1000 m d'altitude, les peuplements sont moins utilisés lorsque l'altitude augmente, et la qualité de l'habitat (taille des arbres, disponibilité des plates-formes, tapis d'épiphytes) a tendance à diminuer avec l'altitude. La pente et l'aspect ont des effets variables : de nombreux nids se trouvent sur de fortes pentes, et le taux de réussite de la nidification dans la baie Desolation Sound augmente en fonction de la pente, mais celle-ci n'est pas nécessairement un bon indicateur d'habitat propice. Les résultats sur les effets de bordure sont contradictoires : beaucoup de nids sont situés à proximité de bordures de forêt; certains des

prédateurs de nids étaient plus nombreux à la lisière des forêts, en particulier à proximité des activités humaines; une étude a révélé une baisse du taux de réussite de la nidification près des bordures, tandis qu'une autre menée dans la baie Desolation Sound n'a révélé aucun effet négatif près des bordures et un taux de réussite de la nidification plus élevé à proximité des lisières naturelles. Les résultats de six études, dans lesquelles on a utilisé le radar, montrent que les populations de guillemots du bassin sont directement proportionnelles aux superficies des vieux peuplements, et certaines études établissent une relation entre des déclins de population et la perte d'habitats. Quant aux densités des oiseaux, elles sont plus grandes dans l'ouest de l'île de Vancouver $(0.082 \pm 0.034 \text{ oiseau par hectare d'habitat propice})$ que sur la côte continentale de la Colombie-Britannique $(0.028 \pm 0.019 \text{ oiseau par hectare})$. Les habitats marins des guillemots varient considérablement, mais ils sont situés en général dans les eaux peu profondes (< 30 m) et abritées ou à moins de 0,5 km des côtes exposées. Ces oiseaux se nourrissent surtout de poissons se rassemblant en bancs et de macro-zooplancton. Les déversements accidentels d'hydrocarbures, les filets maillants, la pêche à la senne coulissante, la pêche à la ligne récréative et l'aquaculture sont des menaces pour ces oiseaux marins; toutefois, leurs impacts sont peu connus en Colombie-Britannique. Les effets des contaminants chimiques (p. ex. les organochlorés, les dioxines, les furannes, les BPC et les métaux lourds) sur le guillemot n'ont pas été étudiés. Rien n'indique d'effets négatifs de maladies, de parasitisme, d'introduction d'espèces ou de surpêche des espèces consommées par le guillemot en Colombie-Britannique.

MARBLED MURRELET CONSERVATION ASSESSMENT - BIOLOGICAL REVIEW

V

Foreword

This review document is Part A of a three part Conservation Assessment for the Marbled Murrelet that was initiated by the Canadian Marbled Murrelet Recovery Team. Parts B and C of the Conservation Assessment deal with conservation and management issues and risk analysis, respectively. The review was funded jointly by the Canadian Wildlife Service, British Columbia Ministry of Water, Land and Air Protection, and Ministry of Forests. The Marbled Murrelet Recovery Team has reviewed and approved the document and comments from three anonymous external expert reviewers were incorporated. I thank the author, contributors, members of the Recovery Team and the external reviewers for their cooperation and patience in the development of this comprehensive scientific review document.

Douglas F. Bertram, Chair Canadian Marbled Murrelet Recovery Team

July 2002 Institute of Ocean Sciences, Sidney, British Columbia

Executive Summary

- 1. The Marbled Murrelet (*Brachyramphus marmoratus*) is listed as Threatened in Canada and is on the provincial Red-list in British Columbia. The species is also listed as Threatened in Washington, Oregon and California, and its status in Alaska is under review.
- 2. This review is part of a Conservation Assessment on the Marbled Murrelet in BC which is being undertaken by the Canadian Marbled Murrelet Recovery Team with the support of the Canadian Wildlife Service, BC Ministry of Water, Land and Air Protection, BC Ministry of Forests and many researchers and wildlife managers in BC. The Conservation Assessment will help the revision of the Marbled Murrelet Recovery Plan and also suggest changes to the Identified Wildlife Management Strategy (IWMS) in the BC Forest Practices Code. This review focuses on biological information relative to the conservation and management of the species in BC. Other parts of the Conservation Assessment deal with management recommendations and risk modeling of management options.
- 3. Marbled Murrelets are members of the seabird family Alcidae, and like other alcids they forage by diving, using their wings for underwater propulsion. Adaptations for this lifestyle affect their flying abilities, flight speed, vulnerability to predators and access to nest sites.
- 4. The species' range extends from the outer Aleutian Islands across southern Alaska and south as far as central California. Within this range there is no evidence of significant genetic differentiation, apart from minor differences in the small populations in the outer Aleutians. Ground-nesting and tree-nesting murrelets in Alaska show no significant genetic differentiation. There is evidence of localized morphometric differences among some BC populations.
- 5. Marbled Murrelets eat many species of schooling fish and large crustaceans, but utilize predominantly sand lance (*Ammodytes hexapterus*) and juvenile herring (*Clupea harengus*) when breeding. They carry a single prey item in their beaks to feed nestlings, and select larger sand lance and other fish for this purpose.
- 6. Migratory movements are poorly known. One banded bird which bred in Desolation Sound, BC, wintered in the San Juan Islands, Washington. Other movements are inferred from seasonal changes in local populations. Birds leave exposed areas on the outer BC coast to overwinter in more sheltered waters.
- 7. Causes of mortality are poorly known. Predation is the main cause of nest failure, and predators at nest sites include accipiters, owls, and corvids (crows, ravens and jays). Corvids are the most common and widespread predators and their numbers have increased over the past few decades in the Pacific Northwest. Squirrels and other arboreal mammals are also suspected predators, especially of nestlings. Rates of predation on adult murrelets are not known, but known predators include falcons, accipiters, and ravens inland, and falcons, Bald Eagles (*Haliaeetus leucocephalus*), large gulls, and sea lions at sea. The dispersed and secretive nesting habits and camouflaged breeding plumage indicate that predation has strongly influenced the evolution of the murrelet's breeding biology.

- 8. Oil spills, gill nets and angler's hooks are known to kill Marbled Murrelets at sea, and the species is among the most vulnerable of seabirds to oil spills (see points 27 and 28 below). There is no evidence of widespread starvation at sea, but murrelets are sensitive to changes in prey availability (see point 25).
- 9. The demographic characteristics of the murrelet are poorly known but the Desolation Sound study is providing valuable data. Measures of demographic parameters include:
- Mean age of first breeding. This is not known. Comparisons with other species and some morphological data suggest that breeding begins at ages 2-5 years. It is likely that the proportion of breeders increases with age within this range.
- Fecundity, defined as the number of female fledglings raised per female of breeding age, has been estimated from observations at nests and counts of juveniles and adults at sea. Estimates of fecundity in Desolation Sound ranged from 0.17 to 0.22 from studies of nesting success and radio-telemetry, and 0.13 from adjusted counts of juveniles and adults at sea.
- Survival of adults. Mark-recapture studies in Desolation Sound indicate local annual adult survival of 0.83 (95% confidence interval 0.72-0.90; combined mist-net and dip-net methods) or 0.92 (95% C.I. 0.63-0.99; mist-net sample only).
- Survival rates of immature birds are not known but are being studied.
- Generation time was estimated from other demographic data to range from 7-13 years with the most reasonable estimate being 10 years.
- The proportion of mature adults in the population is not known but estimates include 85% from a sample of dissected birds off Langara Island, BC, and 55-95% based on females showing raised plasma vitellogenin, brood patches and breeding behaviour in Desolation Sound.

These parameters have been used to model population dynamics (see next point).

- 10. Two pilot population models using available estimates of fecundity, survival and age of first breeding suggested that Marbled Murrelet populations in most parts of North America were declining. Recent models of the Desolation Sound data suggest that the rate of population growth (λ) ranges between 0.93 (declining population) to 1.02 (increasing population), depending on the parameters used. All models indicate that changes in the survival of adult murrelets potentially have greater effects on populations than changes in survival of immatures or in nesting success, but this does not necessarily mean that adult survival is currently limiting murrelet populations.
- 11. The current population of Marbled Murrelets in BC was estimated from recent at-sea and radar counts. Over 32,500 birds were actually counted, and the likely population is between 55,000 and 78,000 (median estimate about 66,000 birds or 56,000 adults if 85% are mature adults). Many parts of the BC range have not been adequately censused, and there is much uncertainty in these estimates.
- 12. There are few data to assess population trends in BC. Anecdotal evidence suggests major declines in the Georgia Depression area (eastern Vancouver Island and the southern mainland). There is also evidence of declines since the late 1970s off southwest Vancouver Island, but these trends are difficult to separate from temporary negative effects of warm ocean conditions. At-sea

surveys in Laskeek Bay (Queen Charlotte Islands/Haida Gwaii) in 1990-1998 show no significant trends. The amount of apparently suitable nesting habitat has dramatically decreased in many areas of the province, and because populations seem correlated with habitat area (see point 19 below), murrelet populations are likely to have decreased as well.

- 13. Recent data indicate a population of 18,000 murrelets in Washington, Oregon and California (95% confidence limits 13,000-23,000). All of these southern populations have been reduced by the effects of logging. Populations in Alaska are difficult to census and estimates range from 280,000 to 1,062,000 birds. There is evidence that murrelet populations are declining in parts of Alaska, especially in the well-studied population in Prince William Sound. Here the combined effects of the *Exxon Valdez* oil spill and long-term changes in food availability are thought to be responsible for the decline.
- 14. The inland breeding habitats of Marbled Murrelets in BC and elsewhere in their range are reviewed at three spatial scales: nest sites (microhabitat), stand-level, and landscape-level. At the nest site level, most nests were on large limbs (15-75 cm diameter) in large, old-growth conifers. Tree species preference varied among study areas and is not a reliable indicator of suitable habitat. Nest trees were typically larger and often provided more platform limbs than other trees nearby. Cliffside ground-nests found in BC and Alaska usually provided mossy nest platforms, overhead cover and flight access similar to those on large trees. Ground nesting is rare in BC and management efforts should be directed at maintaining the most widely used nesting habitat in old-growth conifers.
- 15. Many studies assessed stand level habitat associations, either comparing stands with nests with randomly-selected stands, comparing occupied stands with those showing no occupancy, or using audio-visual detections as indicators of relative abundance. There was considerable variability among these studies but murrelet nesting, occupancy and high levels of activity were frequently positively associated with:
 - tree diameter at breast height (DBH)
 - density of large trees (DBH >80 cm) per hectare;
 - variation in tree size (DBH or height)
 - epiphyte cover on branches;
 - epiphyte thickness;
 - density of potential platforms per ha;
 - density of trees with platforms.

and generally negatively associated with:

- elevation (elevation below 600 or 900 m preferred);
- forests on the coastal fringe (within ca. 500 m of exposed coasts).

Slope and aspect showed variable effects – positive in some areas and neutral or negative in other areas.

- 16. An analysis of 45 nests located by telemetry in Desolation Sound indicated some important stand-level features. Forest polygons containing nests were compared with randomly-selected bordering polygons with trees (treed) or with platform limbs. Polygons with nests were found to:
 - be in older stands of trees:

- have larger mean basal area of trees;
- have greater vertical complexity in canopy structure.

Models of these data indicated that, relative to random polygons (treed or with potential platforms), nest polygons tended to be less uniform with more canopy gaps, and greater vertical complexity in the canopy. These habitat models gave similar results to other models derived from audio-visual and forest structure data.

- 17. At the landscape level, areas with evidence of occupancy tended to have higher proportions of large, old-growth forest, larger stands and greater habitat complexity, but distance to the ocean (up to about 60 km) did not seem important, apart from some avoidance of coastal fringes. Elevation had significant negative effects in some studies but not all.
- 18. Landscape-level analyses of 81 nest sites found by telemetry in Desolation Sound focused on the effects of slope, elevation and aspect. Models of the data showed that slope had a strong positive effect (more nests with increasing slope), elevation a less consistent effect (+ve in some models and –ve in others), and aspect was seldom selected as significant. Nest sites on steeper slopes and at higher elevations were less accessible to people on the ground than those on gentle, lower-elevation slopes. Nest success increased with increasing elevation and increasing slope. Most nests in Desolation Sound were in small old-growth patches (often <50 ha or smaller). In this area, murrelets nesting early in the season tended to travel further from foraging areas to nest, nested on steeper slopes, and had higher breeding success than those nesting later.
- 19. Radar counts of murrelets indicate the value of each watershed as nesting habitat, and show watershed-level habitat associations. Five radar studies in BC and one on the Olympic Peninsula showed significant positive correlations between numbers of murrelets and areas of suitable habitat per watershed, although the measures of habitat differed among the studies. These data provide the first strong evidence that the watershed populations of Marbled Murrelets are directly proportional to the areas of old-growth forest available. There was no evidence that murrelets pack into remnant old-growth patches in higher densities as areas of old growth are reduced by logging. Breeding populations of murrelets are predicted to decline as areas of old-growth decrease. Densities (murrelets per area of habitat) were significantly higher on the west of Vancouver Island $(0.082 \pm 0.034 \text{ SD})$ birds per ha) than on the BC mainland coast (0.028 ± 0.019) birds per ha) when the habitat classified as good was considered in each study.
- 20. Several models or algorithms have been developed which combine habitat measures to classify and map large areas. Some algorithms combined measures derived from canopy structure, elevation, distance from ocean and from forest edges. Others used biogeoclimatic units (e.g., Broad Ecosystem Units) and forest cover maps, either separately or in combinations. Several studies have done ground-truthing to assess the validity of their algorithms and found them to be reasonably reliable in predicting suitable nesting habitat. The use of algorithms to classify habitat is best done using regionally-specific algorithms, combined with confirmation of habitat suitability using helicopters and/or ground surveys.
- 21. The effects on murrelets of fragmentation of forests and the creation of artificial forest edges (e.g. at clearcuts and roads) are reviewed. Important points include the following:

- Many nests were near natural and man-made forest edges. It is not clear whether murrelets
 consistently prefer to nest near edges in all habitats, or whether they are attracted to edge
 habitat by ease of access.
- Clearcut logging changes the microclimate near abrupt forest edges. This might affect nest microhabitats (e.g., moss cover on branches), but this has not been studied.
- Edges affect predation risk. Fragmentation and creation of abrupt forest edges is likely to increase predation risk from corvids, especially Steller's Jay (*Cyanocitta stelleri*). Several studies showed that this jay is most often found close to forest edges bordering clearcuts, and is more abundant in fragmented forest than in contiguous forest. The effects of forest fragmentation on other predators, such as squirrels and raptors, are less obvious or not significant. Murrelets sympatric with Northern Goshawks (*Accipiter gentilis*) might suffer greater predation if both species are forced to share remaining patches of old-growth in heavily logged areas. Proximity to human activities, and the age and structure of forests bordering old-growth also affect abundance of predators.
- Nest success relative to forest edges shows inconsistent trends. In a sample of murrelet nests from across the Pacific Northwest, nests within 50 m of a forest edge had lower success than those >50 m from an edge (38% and 55%, respectively, n = 29 in each sample), although this was not statistically significant. Successful nests were significantly further from edges (mean 141 m) than failed nests (mean 56 m). In contrast, analysis of 98 nest sites in Desolation Sound showed that sites adjacent to natural edges appeared to have higher success than those in the forest interior, and there were no significant differences between nest sites adjacent to artificial vs. natural edges, and artificial edges vs. interior forest.
- Simple geometric models of the possible effects of edges, relative to forest patch area, suggest that effects restricted to 50 m of artificial edges would affect a progressively larger portion of the forest as patch areas declined below 200 ha. Likely effects on breeding success would increase most rapidly as patch areas declined below about 50 ha. The shape of the forest patch also affects the proportion of edge habitat, and the proportion of the patch bounded by natural edges would modify edge effects.
- The type of edge (natural vs. man-made) and the habitat bordering an old-growth patch (e.g., recent clearcut or maturing forest) appear to affect nesting success and predation risk, and need to be considered in planning protected habitats for murrelets.
- 22. Nesting murrelets showed the following relationships with elevation:
- In BC murrelet nests are known from sea level to about 1500 m in elevation. Among 119 nests found by telemetry in BC, 84% were found below 1000 m, and there was a rapid drop-off in nests with increasing elevation above 1000 m. Low-elevation habitat (<600 m) is greatly reduced in Desolation Sound, which provided the bulk of the nests (83). Comparison of nest placement *vs.* distribution of forests in Desolation Sound indicates proportionately higher use of forests between 200-600 m. Outside Desolation Sound, in Mussel Inlet, Clayoquot Sound and Haida Gwaii, 75% of the telemetry nests were below 600 m and all were below 900 m.
- Audio-visual surveys show declining evidence of occupancy of murrelets with increasing elevation. Highest rates of occupied detections were usually in valley bottoms and lowelevation slopes.

- Stand-level and micro-habitat features important for nesting (e.g., large trees, presence of potential platform limbs, epiphyte cover on branches) usually decline with increasing elevation. The only exceptions are in areas where low-elevation old-growth is depleted, and the remaining low-elevation patches appear to provide less suitable habitat for murrelets (e.g., Desolation Sound, southeastern Vancouver Island).
- Landscape-level analyses using a variety of methods generally report negative associations of murrelet detections or measures of suitable habitat with elevation in BC, Washington, Oregon and California.
- Watershed-level radar counts of murrelets on Vancouver Island were more strongly correlated with low-elevation old-growth forest below 600 m than with high elevation forest area or with the full range of forests.
- Although abundance of predators varied with elevation, some species preferred lower and
 others higher elevations. Avian predators declined with elevation in Desolation Sound.
 Overall, there are insufficient data to conclude that predation risk for murrelets consistently
 changes with elevation.
- In Desolation Sound nesting success increased with increasing elevation. The cause of this pattern is not known, but likely linked with increased predation in low elevations. There are no comparative studies of nest success *vs.* elevation from elsewhere.
- In general, optimal nesting conditions in BC are likely to be found at 0-900 m elevation (perhaps 0-600 in watersheds with more intact old-growth stands), less suitable conditions at 900-1500 m, and areas above 1500 are unlikely to be used. In all cases elevation should not be the sole criterion for establishing suitability, and evidence of nesting, occupancy and/or suitable habitat (e.g., potential nest platforms) is needed for establishing habitat suitability.
- 23. Review of the effects of slope and aspect on murrelets indicates the following:
- Marbled Murrelets readily nest on steep slopes, and in Desolation Sound and Mussel Inlet most nests found with telemetry were on steep slopes (30-70°), where much of the forest occurred. In Clayoquot Sound and Queen Charlotte Islands/Haida Gwaii murrelets nested on flat ground and more moderate slopes (all telemetry nests <40°). Many nests have also been found in valley-bottom habitat by ground searches and tree climbing in BC and elsewhere in North America.
- In Desolation Sound success of nests found by telemetry increased with increasing slope. The cause of the trend is not known, but might be linked with the trend for early-nesting, more successful birds to travel further inland than late birds. There are no comparative data from elsewhere on the effects of slope on nest success.
- It is not clear whether steep slopes necessarily provide the best habitat in situations where there is still suitable habitat available on valley bottoms or gentle slopes. Studies made in many areas where such habitat is still abundant (Clayoquot Sound, Carmanah-Walbran, Queen Charlotte Islands/Haida Gwaii) tend to show negative or non-significant associations between slope and murrelet occupancy, or measures of habitat suitability. Even in Desolation Sound, occupancy of stands was negatively associated with slope.
- Steeper slopes are presumed to benefit murrelets by making it easier for them to access the mid- to lower-crowns of the trees where larger branches occur. Slopes are not essential if the forest canopy is variable and/or has gaps to provide similar accessibility. Several studies have

- shown positive associations between nesting murrelets and variable canopy structure and/or gaps in the forest.
- Given the inconsistency in data on slope, it seems prudent to avoid including slope as a strong predictor (+ve or -ve) of suitable habitat in BC. Instead, management and mapping should focus on forest structure, measures of canopy accessibility, and nest site attributes known to be reliable indicators (e.g., presence of platform limbs and epiphyte cover).
- Aspect does not appear to have a strong effect on the placement or success of nests, although south-facing slopes in drier areas appear to have fewer mossy platforms than other aspects.
- 24. Radio-tracking studies from Desolation Sound, Toba Inlet, Mussel Inlet, Clayoquot Sound and in California indicate a relationship between the area where birds are caught and those where they are found nesting. In all 5 areas, nest distributions formed wedge-shaped areas inland, up to 50 km deep, from marine capture sites. Murrelets tend to feed in productive areas close to nesting habitat but sometimes commute large distances (occasionally more than 100 km) to feed at prey concentrations
- 25. Marine habitats used by Marbled Murrelets vary considerably, but some preferences are evident. Along exposed shores, murrelets tend to remain within 0.5 km of shore, but in sheltered waters they often range several km offshore. Most foraging is done in relatively shallow water (<30 m), and is often associated with sandy or gravel substrates which shelter sand lance fish. Murrelets frequent tidal rips and upwellings in some areas but avoid them in others. Their distribution relative to sea temperature and salinity is complex and few generalities emerge; e.g., aggregations are associated with warm water in some areas and cold water in others. Several studies report diurnal and seasonal shifts in habitat use. In all marine habitat assessments, the effects of spatial and temporal scales need to be considered; patterns evident at small scales might not be evident at larger ones (and *vice versa*).
- 26. The effects of multi-year variations in ocean conditions on Marbled Murrelets have received little attention, but are potentially important. These variations include El Niño and La Niña events, 15-20-year Pacific Decadal Oscillations, and global climate change. Murrelets appeared to be negatively affected by unusually warm seas off southwest Vancouver Island in the 1990s. Murrelets in parts of Alaska seem to be declining as a result of ocean conditions unfavourable for forage fish, suggesting that food availability, rather than nest sites, is currently the limiting factor for these populations. It is not known whether similar limitations apply to any areas in BC.
- 27. Threats to the BC population are reviewed. There is no evidence that disease, parasitism, introduced species, or over-fishing of prey have serious affects on the BC population. Predation is evidently important (see points 7 and 21 above). Interspecific competition from predatory fish (mackerel) might reduce prey availability during periods with warm oceans.
- 28. Gill-nets and, to a lesser extent, purse-seining, sports angling and aquaculture, are threats to murrelets, but their impacts in BC are poorly known. A study in Barkley Sound in 1979-1980 found that gill-nets killed 6% of the local breeding population, but there appears to be less mortality there in recent years. Methods for reducing seabird by-catch in gill-nets have been

developed in Washington and need to be considered in BC. Research on by-catch has started in BC.

- 29. Marbled Murrelets are among the seabirds most vulnerable to oil spills, because they remain at sea most of their lives in nearshore areas near shipping lanes and other sources of oiling. Major oil spills killed hundreds of murrelets off BC and Washington (*Nestucca* and *Tenyo Maru*), and thousands in Alaska (*Exxon Valdez*). Low-level chronic oil pollution is also likely to kill murrelets, but current data suggest that this is not a major cause of mortality in BC.
- 30. The effects on murrelets of other chemical contaminants (e.g., organochlorines, dioxins, furans, PCBs, heavy metals) have not been studied. Although the levels of these toxins in other fish-eating birds in BC have declined through the 1980s and 1990s, some contamination persists and sometimes reaches levels which can negatively impact the birds. The Strait of Georgia and Puget Sound, where many murrelets breed and even more overwinter, remain among the most polluted waters in the murrelet's range. Low-levels of contamination might act as endocrine disrupters, causing reductions in breeding performance which might be hard to detect.

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ACRONYMS AND TECHNICAL TERMS USED IN THIS REPORT

AHY	After-hatching-year age class - includes all birds more than one year old, whether mature or immature
Algorithm (habitat)	Mathematical model, equation, or series of equations used to predict the suitability of an area as potential habitat for a species
Alternate plumage	Plumage assumed during the breeding season (also known as breeding or summer plumage). In Marbled Murrelets some of the birds in alternate plumage are immatures older than one year which assume breeding plumage but do not breed (see also Basic Plumage and AHY)
ANOVA	Analysis of variance statistical test
At-sea fecundity	Fecundity measured at the time the murrelet fledgling arrives at sea (see also Fecundity and Nest Fecundity)
Basic plumage	Plumage assumed outside the breeding season (non-breeding or winter plumage). See also Alternate plumage.
BEC	Biogeoclimatic ecosystem classification
Biogeoclimatic subzones and variants	Subzones and subzone variants of the Biogeoclimatic zones used in BC (see Green and Klinka 1994:34). The following are mentioned in this report:
	CDFmm – Coastal Douglas-fir Moist Maritime subzone
	CWHvh1 – Coastal Western Hemlock Southern Very Wet Hypermaritime variant
	CWHvh2 – Coastal Western Hemlock Northern Very Wet Hypermaritime variant
	CWHvm1 – Coastal Western Hemlock Submontane Very Wet Maritime variant
	CWHvm2 - Coastal Western Hemlock Montane Very Wet Maritime variant
	CWHwh1 – Coastal Western Hemlock Submontane Wet Hypermaritime variant
	CWHwh2 – Coastal Western Hemlock Montane Wet Hypermaritime variant
	CWHxm – Coastal Western Hemlock Very Dry Maritime subzone
	MHmm1 – Mountain Hemlock Windward Moist Maritime variant
	MHmm2 – Mountain Hemlock Leeward Moist Maritime variant
	MHwh – Mountain Hemlock Wet Hypermaritime subzone
CDF	Coastal Douglas-fir biogeoclimatic zone (see Biogeoclimatic subzones & variants)
CI (95% CI)	Confidence interval (or confidence limits) – range of values for a parameter in which there is 95% confidence of including the mean for the statistical population

COSEWIC Committee on Status of Endangered Wildlife in Canada - a joint federal-

provincial body which decides on the lists of endangered and

threatened species in Canada

CWH Coastal Western Hemlock biogeoclimatic zone (see Biogeoclimatic

subzones & variants)

CWS Canadian Wildlife Service (Environment Canada)

DBH Tree diameter at breast height

DDD Organochlorine insecticide similar to DDT

DDE Breakdown product of DDT

DDT Dichloro-diphenyl-trichloroethane (organochlorine insecticide)

ENSO El Niño-Southern Oscillation – the process responsible for producing El

Niño (exceptionally warm) and La Niña (exceptionally cool) ocean

conditions

Fecundity The annual number of female offspring which reach independence

(fledge) per female of breeding age, including any attempts to re-lay after losing a clutch (see also At-sea Fecundity and Nest Fecundity)

Generation time Mean number of years elapsing between the birth of parents and the birth

of offspring - depends on the age of first breeding and annual survival

GIS Geographic Information System

Habitat Mapping which considers the potential for polygons to develop suitable

capability habitat in the future (after logging or other disturbance). See also

mapping Habitat Suitability mapping.

Habitat Mapping which considers the present age and integrity of the vegetation to

suitability decide whether or not the habitat is suitable for a species. See also

mapping Habitat Capability mapping.

HCB Hexachlorobenzene (an organochlorine chemical)
HCH Hexachlorocyclohexane (an organochlorine chemical)

HSI Habitat Suitability Index model

Hatch-year age class (i.e., Juvenile) – bird less than one year old

HY:AHY ratio Ratio of birds in hatch-year (Juvenile) plumage to birds in alternate

plumage recorded during at-sea surveys (see HY and AHY) and used

as an index of breeding productivity

Immature Bird which has not attempted breeding

IWMS Identified Wildlife Management Strategy – the portion of the BC Forest

Practices Code which provides procedures and measures for the management of species at risk which require special management

attention (Anon. 1999)

Juvenile Bird within its first year of life

Lambda (λ) Symbol used as the measure of the annual rate of population growth. If λ

equals 1 the population is stable, if λ is less than 1 the population is

declining, and if λ is greater than 1 the population is increasing

Local survival Survival from one year to the next within the study area - includes

possible permanent emigration, and also possible effects related to

capture and marking (see True Survival)

LU Landscape Unit (usually 30,000 to 150, 000 ha and covers one to several

watersheds)

Bird which has attempted breeding Mature bird

Mountain Hemlock biogeoclimatic zone (see Biogeoclimatic subzones & MH

variants)

MMRT Marbled Murrelet Recovery Team (Canada)

BC Ministry of Forests **MOF**

MWLAP BC Ministry of Water, Land and Air Protection

Non-contributing Land Base – land classified as not contributing to the NCLB

Timber Harvesting Land Base (see THLB)

Fecundity measured at the point of the fledgling's departure from the nest Nest fecundity

(see also Fecundity and At-sea Fecundity)

Nesting success The number of fledglings per pair of adult birds that attempt breeding **OGMA**

Old Growth Management Area – area set aside for maintaining the

biodiversity attributes of old-growth forests

PCBs Polychlorinated biphenyls

Polychlorinated dibenzo-dioxins (often simply referred to as dioxins) **PCDD** Polychlorinated dibenzo-furans (often simply referred to as furans) **PCDF**

PDO Pacific Decadal Oscillation – long-term trends in oceanic conditions in the

North Pacific (usually seen as alternate warm and cool cycles each

lasting approximately 20 years)

Queen Charlotte Islands (also known as Haida Gwaii) OCI

Red-listed A species legally designated or being considered for legal designation as Endangered or Threatened within the Province of British Columbia species

Resource Inventory Committee (Province of British Columbia) **RIC**

Standard deviation SD SE Standard error

Sensitive ecosystem inventory – identified and mapped sensitive SEL

ecosystems in BC

SFU Simon Fraser University

Sea surface salinity (measured in parts per thousand) SSS

SST Sea surface temperature (degrees Celsius)

TBT Tributyltin – often used as an anti-fouling agent in marine paint

TEM Terrestrial ecosystem mapping using ecosystem units

Tree Farm Licence TFL

THLB Timber Harvesting Land Base – land classified as suitable for timber

harvesting (see NCLB)

Terrain Resource Information Management (shows contour lines, streams TRIM

etc.)

True survival	Defined as the survival of birds from one year to the next and excluding migration effects and effects of capture and marking (see Local
	Survival)
UBC	University of British Columbia
UVic	University of Victoria
Vitellogenin	A protein destined for egg yolk, measured in blood plasma and used as an indicator of female birds likely to lay an egg
VRI	Vegetation Resources Inventory - forest cover mapping based on air photo interpretation and topographic mapping
WHA	Wildlife Habitat Area – area designated for the protection of a species under the Identified Wildlife Management Strategy (see IWMS)

1 INTRODUCTION

The Marbled Murrelet (*Brachyramphus marmoratus*) is rapidly becoming one of the most studied seabirds in North America. This is due to its listing as Threatened through most of its range, the amount of research needed to understand its complex marine and terrestrial habitat relationships, and its interaction with the forest industry along most of the forested Pacific coast of North America. This review, part of a Conservation Assessment of the Marbled Murrelet in British Columbia, is an attempt to summarise most of the pertinent biological information that applies to the conservation and management of the species in the province. Other parts of the Conservation Assessment will use this information to develop management and conservation strategies (see below).

Status of the Marbled Murrelet in Canada (British Columbia) - Marbled Murrelets were listed as Threatened by COSEWIC (Committee on Status of Endangered Wildlife in Canada, a joint federal-provincial body) in 1990 (Rodway 1990). Loss of nesting habitat in forests, and threats posed by oil spills and gill nets were given as the main threats. Following a second review (Hull 1999), this status was confirmed again in 2000, primarily on the basis of low reproductive rate and continued evidence of declining nesting habitat (D. Fraser, pers. comm.). Provincially, the Marbled Murrelet is on the Red-list (species legally designated or being considered for legal designation as Endangered or Threatened). The murrelet is one of the Identified Wildlife species within the BC Forest Practices Code Act. The Identified Wildlife Management Strategy (IWMS; Anon. 1999) mandates the creation of Wildlife Habitat Areas (WHAs) for Marbled Murrelets. Provisions contained in the Landscape Unit Planning Guide under the Forest Practices Code place restrictions on the way in which WHAs for Marbled Murrelets can be designated.

Reasons for the Conservation Assessment and Biological Review - The Conservation Assessment is being done under the direction of the Canadian Marbled Murrelet Recovery Team (MMRT), and funded by Environment Canada (Canadian Wildlife Service), BC Ministry of Water, Land and Air protection (MWLAP), and BC Ministry of Forests (MOF). The Conservation Assessment was required for several reasons:

- to form the basis for a revised national Marbled Murrelet Recovery Plan;
- as part of the review of the provincial Identified Wildlife Management Strategy (IWMS) within the BC Forest Practices Code (Anon. 1999);
- to provide a summary of relevant information to wildlife and forest managers and others involved in the conservation and management of Marbled Murrelets.

Each of these points requires some explanation.

Following the designation as Threatened by COSEWIC, a Recovery Plan for the Marbled Murrelet was completed in 1994 (Kaiser et al. 1994) which focussed primarily on the research needed to fill the many information gaps concerning the species. A second COSEWIC review was completed in 1999 (Hull 1999), which prompted a more comprehensive Conservation Assessment in 2000-2001(details below). The MMRT plans to complete a revised Recovery Plan in 2001-2002.

Most of the nesting habitat of Marbled Murrelets in BC is controlled by the province. The primary process for protecting some of this habitat is through the BC Forest Practices Code Act, and specifically through the Marbled Murrelets account within the IWMS (Anon. 1999). The IWMS account is scheduled to be reviewed in 2002 and the Marbled Murrelet Conservation Assessment will be part of that review. The main conservation process for murrelets within the existing IWMS account is protection of 10-12% of the Landscape Unit's original suitable nesting habitat, within 85 km of the sea, and preferably situated within contiguous blocks of 200 ha or larger (Anon. 1999). Environmental groups and some research biologists have raised concerns that leaving only 10-12% of the original nest habitat will cause significant declines in the population. Wildlife Habitat Areas (WHAs) are usually set up through consultation involving MWLAP, MOF and the affected forest companies.

Application of the IWMS provisions for Marbled Murrelets potentially represents one of the largest non-timber constraints on timber harvesting within the Forest Practices Code. A Memorandum of Understanding (April 1999) between the Ministry of Environment, Lands, and Parks (now Ministry of Water, Land and Air Protection) and the Ministry of Forests integrated WHAs and establishment of Old Growth Management Areas (OGMAs) into Landscape Unit Planning. The memorandum directed the placement of Marbled Murrelet WHAs into Non-Contributing Forest (forested Crown land that does not contribute to the Allowable Annual Cut but that does contribute to seral stage and old growth retention targets). This directive and the IWMS requirements are proving difficult to implement, because available patches of suitable habitat, especially those in non-contributing forest, often do not meet the IWMS requirements. Analyses outlining the difficulties of establishing WHAs under the current constraints have been done for the Sunshine Coast (Manley and Jones 2000, Jones 2000, Jones and Manley 2001), Vancouver Island (Mather and Chatwin 2001), and the Eden landscape unit in Queen Charlotte Islands/Haida Gwaii (Anon. 2001).

One reason for the present review is to address the thorny questions of how the location, size, shape and composition of WHAs (and other protected areas) might affect murrelets. Other critical management concerns addressed in this review are whether reduction of forest habitat will necessarily lead to a reduction in populations, and how fragmentation of forests affects murrelets.

A major goal of the review is to provide biologists and managers with a comprehensive summary of relevant information, summarised in sufficient detail but without lengthy details of methodology and statistics, and citing all the necessary references. Statistical tests are given here only when they are not available in the cited references. The multi-authored compendium produced by Ralph et al. (1995a) and the more condensed review by Nelson (1997) remain excellent resources, but there has been much ground-breaking research in BC and the U.S. since their publication. This review is therefore an attempt at updating these publications with information relevant to BC.

Outline of the Conservation Assessment Process – The 2001-2002 Conservation Assessment is a multi-stage process involving these steps:

- a compilation and summary of relevant research and management reports from BC for the period 1991-1999 (completed: Hooper 2001);
- a review of the general biology, populations, habitat associations, and conservation of the murrelet, relevant to BC (Part A this report);
- a statement of conservation and management objectives focused on the needs of the murrelet (Part B by the Marbled Murrelet Recovery Team);
- a risk-analysis of management options (Part C facilitated by D. Steventon of MOF, G. Sutherland of Cortex Consultants, and P. Arcese of UBC);
- analysis of economic and social impacts (MOF headquarters);
- revision of the Marbled Murrelet Recovery Plan (Marbled Murrelet Recovery Team);
- review of the IWMS requirements applicable to Marbled Murrelets (MWALP and MOF);
- review of the requirements applicable to Marbled Murrelets under the incoming Species at Risk Act (Environment Canada CWS).

Criteria for the review - This review covers biological issues that affect the murrelet in BC. The primary focus is on factors related to nesting requirements, predation risk, changes in coastal forests, risks of oil spills, gill-netting and other human-related processes at sea, and natural processes (e.g., global climate change) which might affect the status of the BC population over the long-term.

The review builds on the recent compilation of BC research by Hooper (2001), and the COSEWIC review by Hull (1999), and also incorporates the results of research done in Alaska, Washington, Oregon and California which are applicable to BC. Because of the huge volume of publications and reports, much of it unpublished and un-refereed, some selection was necessary to meet the time-lines of the project. Preference was given to studies that had large sample sizes and rigorous quantitative methodology, were multi-year, had widespread application, and had some evidence of outside review. Tables, graphs and other data were included to make the review as comprehensive as possible, and to summarise information that might not be readily available to people working outside universities or research labs.

Much of the information on Marbled Murrelets in BC and the U.S. is in non-refereed, unpublished reports. This includes some of the most valuable information and some excellent studies, and most of these studies were included. There is, however, with un-reviewed reports a greater chance that the analysis, interpretation and conclusions of the study might not be as thorough as in a peer-reviewed publication, and hence more likely to change, or be interpreted differently when revised. Some of the information included in the review has not been published in any format, but is included because of its importance to the project. Where possible, this review cites only material that is in some written form, available for consultation.

To avoid biased interpretation of any studies or unpublished material, original researchers were frequently consulted for explanations of their data, and were provide with drafts for their review and improvement. Two drafts of the review were reviewed by the Marbled Murrelet Recovery Team and many other people experienced with the species in BC (see Acknowledgements). The

entire document was subjected to further peer review by three anonymous experts appointed by the Marbled Murrelet Recovery Team.

2 GENERAL BIOLOGY

2.1 Species description and taxonomy

Marbled Murrelets are members of the family Alcidae (alcids or auks) within the Order Charadriiformes (Gaston and Jones 1998). Alcids are all pursuit-diving seabirds, using their wings to "fly" underwater in search of prey (see below for diet and foraging). In many ways they are the northern equivalents of penguins, with the obvious exception that the extant alcids have retained the ability to fly. Like penguins in the south, the alcids are extremely successful and make up the bulk of seabird biomass in the cool temperate and polar oceans of the northern hemisphere. Being adapted for both underwater and aerial flight, the alcids have reduced wing areas (to reduce underwater drag) and well developed flight muscles. Consequently they are all relatively stocky birds with high wing-loading (ratio of body mass to wing area). This has important consequences for all alcids. Birds with high wing loading require rapid, flapping flight to remain airborne (Pennycuick 1987). Marbled Murrelets typically fly at 70 km/h or faster (Burger 1997a). Such flight is energetically expensive and alcids typically breed in areas of high ocean productivity with concentrated prey. Many alcids, including murrelets (Whitworth et al. 2000, Hull et al. 2001a), commute large distances, sometimes >100 km, to feed at prey concentrations (Gaston and Jones 1998). Changes in the distribution and concentration of prey can cause breeding failure and, in rare cases, adult mortality among alcids.

A second important consequence of having high wing-loading is that alcids cannot take off or land very easily and are vulnerable to predation on land. Most alcids nest on offshore islands relatively free of predators, and nest sites are either on cliffs or in hillside burrows (Gaston and Jones 1998). Although Marbled Murrelets differ in many respects to most other alcids, their choice of breeding site reflects similar constraints imposed by high wing-loading and low maneuverability. The majority of murrelet nests found have been high in the canopy of large coniferous trees, which in many ways resemble cliff-side nest sites. In both cases alcids can approach the nest site at high speed from below and sweep upward to make a stalled landing on the ledge or bough. Conversely, take-off is facilitated by the bird launching itself downward and rapidly gaining the ground speed necessary for controlled flight. Having an uneven canopy structure with gaps in the canopy through which murrelets can make these maneuvers is therefore an important aspect of their preferred habitat.

Phylogenetic relationships within the alcids have been derived from morphological (Strauch 1985) and molecular evidence (Friesen et al. 1996a), giving similar results. Three species are now recognized within the genus *Brachyramphus*: the Marbled Murrelet (*B. marmoratus*), distributed along the North American coast from Alaska through California (details below); the Long-billed Murrelet (*B. perdix*), found in the western Pacific, principally Siberia and Japan; and, Kittlitz's Murrelet (*B. brevirostris*), found in Alaska and usually associated with glacial meltwater (Nelson 1997, Gaston and Jones 1998). The Marbled and Long-billed murrelets were considered to be conspecifics, but molecular studies showed that they are clearly different, and have probably been reproductively isolated for 5-6 million years (Friesen et al. 1996a,b). They

are now treated as separate species (AOU 1997). Long-billed Murrelets occasionally occur as vagrants in North America (Sealy et al. 1991, Mlodinow 1997).

Some intraspecific morphological and molecular variation has been found among populations of Marbled Murrelets (Pitocchelli et al. 1995, Friesen et al. 1996b, Congdon et al. 2000, Hull et al. 2001b), but no subspecies or races are presently recognized. Friesen et al. (1996b) found genetic variation among samples from six sites in Alaska, one in Washington and one in Oregon, but differences among the populations were not consistent for all the molecular tests. Alaska samples were distinct from the single Oregon sample, but other relationships were not supported. The most recent analysis of population differentiation by Congdon et al. (2000) revealed two lineages which apparently diverged prior to the last glaciation. One lineage included murrelets from small isolated populations in the outer Aleutian islands (Attu and Adak), and the other murrelets from mainland Alaska (Alaska Peninsula through southeast Alaska) and British Columbia. Samples from BC (30 birds) showed no differentiation from samples taken from mainland Alaska. Comparisons between ground-nesting and tree-nesting populations in Alaska found few significant morphological differences and no evidence of genetic differentiation (Pitocchelli et al. 1995, Congdon et al. 2000).

The following scenario has been suggested by Congdon et al. (2000) to explain the distribution and genetic variation within Marbled Murrelets:

- population expansion between 800,000 and 80,000 years ago;
- isolation and genetic divergence in two refugia during the late Pleistocene (one in the Bering Sea and one on the North America mainland);
- population expansion and secondary contact following the retreat of the glaciers;
- maintenance of population genetic structure because of the isolation and small population found in the western Aleutians.

Although population differentiation within BC has not been specifically tested, significant differentiation into genetically distinct populations seems highly unlikely, based on the results from Friesen et al. (1996b) and Congdon et al. (2000). Hull et al. (2001b) report some morphological differences among neighbouring populations on the mainland coast of BC.

2.2 Geographical distribution

Marbled Murrelets are restricted to the Pacific coast of North America, with breeding occurring from Attu and other islands of the Aleutian archipelago, through southern Alaska, BC, Washington, and Oregon, to Santa Cruz county in central California (Ralph et al. 1995b, Nelson 1997). The bulk of the population is found in southern and south-eastern Alaska and BC (see Population Size; sections 3.2 and 3.4 below). There are some gaps in this breeding distribution, notably for about 450 km in central California where virtually no suitable inland habitat remains (Nelson 1997, U.S. Fish and Wildlife Service 1997).

The winter range is poorly documented but includes most of the marine areas used in the breeding season, and extends south into southern California (Nelson 1997).

2.3 Diet, nutrition and energetics

The species has a diverse diet, but small schooling fish and large pelagic crustaceans (euphausiids, mysids, amphipods) are the main prey items (see summaries by Sealy 1975a, Carter 1984, Vermeer et al. 1987, Burkett 1995, Nelson 1997, Day and Nigro 2000). The most common fish are Pacific sand lance (*Ammodytes hexapterus*), northern anchovy (*Engraulis mordax*), immature Pacific herring (*Clupea harengus*), capelin (*Mallotus villosus*), and smelt (*Hypomesus* sp.). Squid (*Loligo* spp.), immature salmon (*Oncorhynchus* spp.) and eulachon (*Strongylura exilis*) are also taken in some areas.

In BC the most common prey was sand lance (Burkett 1995), and in many areas the distribution, abundance and movements of murrelets seem closely linked to those of sand lance, especially during the murrelet's breeding season (Sealy 1975a, Carter 1984, Mahon et al. 1992). Unfortunately, little is known about the distribution, densities, diurnal and seasonal movements, or in fact any aspects of the biology of this important feed fish within BC. Robards et al. (1999a) have compiled a comprehensive annotated bibliography on sand lance. Some aspects of its biology can be inferred from general reviews (Field 1988, Robards and Piatt 1999) and work done elsewhere in the North Pacific (Robards et al. 1999a,b,c). Immature herring, and to a lesser extent, salmon smolts and immature rockfish (Scorpaenidae) are important alternative prey in BC. Hay et al. (1989, 1992) and Gillespie and Westrheim (1997) review data on forage fish important to seabirds in BC, and Grosse and Hay (1988) and Hay and McCarter (1997) review herring biology.

Marbled Murrelets usually carry a single prey item to their chicks, and appear to select a large, energy-dense fish for this purpose, typically larger sand lance, immature herring and occasional salmon smolts (Carter and Sealy 1987a, Burkett 1995, Nelson 1997, Jones 2001). In both sand lance and herring, the older classes were both larger and had higher energy contents than the immature 0+ class (Vermeer and Devito 1986, Robards et al. 1999b). Adults are likely to consume smaller items such as immature sand lance and crustaceans, especially in winter and spring in some areas. This pattern of adults taking large prey items back to nest sites but eating large amounts of smaller prey is common among alcid species (Vermeer et al., 1987).

2.4 Foraging behaviour

Like all alcids, murrelets dive using their wings as the primary source of propulsion. The depths at which most foraging occurs are not known, but those killed in gill nets in Barkley Sound were in the upper 3-5 m (Carter and Sealy 1984), and murrelets commonly feed on small schools of sand lance or herring within the upper 5 m of the surface (Mahon et al. 1992, A. E. Burger unpubl. data). An alcid the size of a murrelet is expected to have a maximum diving depth of about 47 m (Mathews and Burger 1998), and the deepest record was one caught in a gill net at 27 m in California (Carter and Erickson 1992).

2.5 Movements, dispersal and home range

Marbled Murrelets are somewhat migratory, but unlike most migrant waterbirds, only a portion of the population appears to leave the breeding grounds. The pattern of movements is poorly

known and appears to vary across the range (Nelson 1997). Most birds which breed on the west coast of Vancouver Island leave the area immediately after breeding in late July through September, and are thought to move to more sheltered waters in the Strait of Georgia and Puget Sound, but some remain through the winter (Burger 1995a). Beauchamp et al. (1999) provided the only evidence to date of migration: an adult banded in Desolation Sound was caught wintering in the San Juan Islands, Washington, and was then recaptured again during the breeding season in Desolation Sound. Other marked murrelets from Desolation Sound, however, appeared to remain there after breeding (Beauchamp et al. 1999). Radio-tagged adults have recently been tracked to moulting aggregations near Desolation Sound (N. Parker unpubl. data).

2.6 Reproduction

Nest sites and nesting habitat are described in section 4 and breeding success, fecundity and factors affecting these are discussed under Demographics (section 3).

2.7 Mortality

2.7.1 Predation

Predation is the best documented cause of mortality, particularly during the breeding season, but its demographic importance, relative to other causes of mortality such as starvation and disease, is not known. Predators of murrelets were summarised by Nelson (1997) and Hooper (2001), and much has been learned about predation risk by the experimental work in Washington and Oregon (Marzluff et al. 2000, Luginbuhl et al. 2001, Raphael et al., in press). At sea, predation by Bald Eagles (*Haliaeetus leucocephalus*), Peregrine Falcons (*Falco peregrinus*), Western Gull (*Larus occidentalis*), and northern fur seal (*Callorhinus ursinus*) has been reported. Sea lions and large fish might also be occasional predators. Known predators of adult birds in forest habitat include Peregrine Falcon, Sharp-shinned Hawk (*Accipiter striatus*), and Common Raven (*Corvus corax*), and remains of murrelets have been found at nests of Northern Goshawks (*Accipiter gentilis*), Bald Eagles and Peregrine Falcons. Common Raven and Steller's Jay (*Cyanocitta stelleri*) are known to have taken eggs and chicks, and Sharp-shinned Hawk to take chicks. Suspected predators at nests include Great Horned Owls (*Bubo virginianus*), Barred Owls (*Strix varia*), Cooper's Hawks (*Accipiter cooperi*), Northwestern Crows (*Corvus caurinus*), American Crows (*C. brachyrhynchos*), and Gray Jays (*Perisoreus canadensis*).

Corvids (ravens, crows and jays) are common nest predators of forest birds, and are probably the most frequent predators of Marbled Murrelet nests. On the Sunshine Coast, Manley (1999) found that 14 (67%) of 21 nesting attempts with known outcome had failed, and predation was responsible for 12 (86%) of the failures. She suspected that Common Ravens predated eight nests and Steller's Jay or Gray Jay another four. Murrelets at two nests flew off when ravens flew over, and both nests were later found to be predated. Populations of several corvid species have increased dramatically in western North America as a result of forest fragmentation, increased agriculture and urbanization (Marzluff et al. 1994). Between 1968 and 1993 breeding bird surveys in coastal British Columbia showed annual increases averaging 5%, 2% and 3%,

respectively, for Common Ravens, Northwestern Crows and Steller's Jays (Campbell et al. 1997).

Predation by mammals at murrelet nests has not been documented, but is thought to be an important cause of nest failure (Nelson and Hamer 1995, Nelson 1997, Manley 1999). An intensive experimental study in Washington and Oregon provides the strongest evidence for this view (Marzluff et al. 1999, 2000, Luginbuhl et al. 2001). This 5-year study combined observations at simulated murrelet nests containing murrelet-sized plastic eggs, dummy chicks or live pigeon nestlings, experiments with captive mammals, and radio-tracking of a large sample of potential predators. Potential predators identified at simulated murrelet nests included Cooper's Hawk, Barred Owl, Steller's Jay, Gray Jay, American Crow, Common Rayen, northern flying squirrel (Glaucomys sabrina), Townsend's chipmunk (Tamias townsendii), Douglas squirrel (Tamiasciurus gouglasi), deer mice (Peromyscus maniculatus and P. keeni), bushy-tailed woodrat (Neotoma cinerea), and an unidentified mustelid (possibly marten Martes americana). Potential predators disturbed 82% of 669 dummy nests in Washington, and 78% of 142 nests in Oregon. Preliminary analysis suggested that about 26% of the contents of dummy nests were preyed upon by corvids (jays, crows and ravens) and 25% by mammals (mostly flying squirrels). Most eggs were lost to corvids and most chicks to small mammals. Other experiments showed that northern flying squirrels were unlikely to be able to break into Marbled Murrelet eggs (Flaherty et al. 2000). Red squirrels (Tamiasciurus hudsonicus) were not encountered or tested in these studies, but this species is known to take eggs and nestlings frequently (Sullivan 1991, Vander Haegen and DeGraaf 1996, Pierre et al. 2001). In the Pacific Northwest old-growth forests several mammals species visit tree canopies, including deer mice (N. Winchester, pers. comm.), and squirrels can occur in high densities there (Carey 1995, 1996). On Vancouver Island, Ethier (1999) found no difference in the relative abundance of red squirrels in old growth and second-growth forests.

The impacts of predation from Northern Goshawks on Marbled Murrelets are poorly understood, but are potentially important to the population dynamics of murrelets. Steven Lewis (Alaska State Fish and Game Department, unpublished data) analysed prey taken by goshawks in southeast Alaska. Marbled murrelets made up 2.8% (10 of 361) of prey remains collected from 28 nests throughout southeast Alaska, and were found at 7 of the 28 nests. Similarly, 3.1% (12 of 382) of prey identified from pellets were murrelets or unidentified alcids likely to be murrelets. Prey deliveries were observed at ten nests throughout southeast Alaska over two years. Marbled Murrelets made up 0.8% (11 of 1451 deliveries) and were delivered to 6 of the 10 nests. Not unexpectedly, most murrelets were delivered early in the morning (9 between 0335 and 0511, one at 0829, and one at 2028). Iverson et al. (1996) reported alcid (mostly murrelet) remains at 20% of 15 goshawk nests in southeast Alaska.

On Vancouver Island, Marbled Murrelet remains were found in 15% of 90 goshawk pellets, and murrelets were ranked fourth in prey species occurrence (Ethier 1999). This indicates that predation by goshawks might be more common than previously suspected. If both goshawks and murrelets are forced by logging practices to nest in the same old-growth patches, then the risks to murrelets would increase considerably. The interactions are, however, complicated by the fact that goshawks also kill many nest predators, which might benefit murrelets. In Ethier's (1999)

sample the most common prey species was red squirrel (69% occurrence in goshawk pellets), and other known or potential predators of murrelets were Steller's Jay (38%), Gray Jay (4%) and Northern Pygmy-Owl (*Glaucidium gnoma*) (1%). Overall, if one considers that each occurrence in a pellet represents a separate animal, for every 14 Marbled Murrelets killed there were 101 potential predators (squirrels, jays, owls) killed by goshawks. Squirrels and jays were also important prey for goshawks in southeast Alaska, and the introduction of red squirrels to some islands might have benefited goshawks there (Iverson et al. 1996).

The absence of goshawks might lead to "mesopredator release", when the decline or absence of larger predators allows an increase in mid-sized predators (such as squirrels and jays), sometimes causing devastating effects on prey populations (Crooks and Soulé 1999). It is not clear whether direct predation of goshawks on murrelet adults has a greater impact on murrelet populations than reductions in nest predation that goshawks might induce by killing squirrels and jays. The loss of an adult bird has a much greater impact on population dynamics than the loss of an egg or chick (see Demographics section 3.1.10), and the relative impacts of losing a few adults or losing a greater number of eggs and chicks have not been analysed. Clearly, the impacts of goshawks and other inland predators on murrelet populations need to be examined in more detail, within the context of reduction and fragmentation of old-growth forests.

The effects of forest fragmentation and edges on predation risk for Marbled Murrelets are discussed in more detail elsewhere (section 4.7).

2.7.2 Other causes of mortality

Starvation at sea is suspected to occur in fall and winter, but is poorly documented, and nothing is known about the effects of disease or parasites (Nelson 1997). Stephen and Burger (1994) investigated likely causes of death in a necropsied sample of 73 seabirds found dead in BC. There were no Marbled Murrelets in this sample, but the study gives a general indication of possible causes of seabird mortality. Causes of mortality included human-induced factors, such as oiling, shooting, and other less common factors (27% of birds), open causes which included probable predation (16%), starvation (18% - most likely an underestimate), gastrointestinal lesions (15%), trauma such as broken bones (10%) infections other than in the gastrointestinal tract (7%), and other causes (10%). Only five Marbled Murrelets were identified among 823 carcasses reported in beached bird surveys covering 38 sites on the BC coast between 1989 and 1993 (Burger 1993a). Four of these were on the west coast of Vancouver Island and one from southern Vancouver Island. Four were found in July and one in November and the causes of death were unknown for all (BC Beached Bird Survey database).

Murrelets at sea have been killed by oil spills, gill-nets and anglers' hooks (see section 6.2). Other documented causes of mortality include collisions with vehicles and transmission wires by low flying adults (Nelson 1997).

Nestlings are known to fall from nests (Binford et al. 1975, Manley 1999), and adults and nestlings die when trees are felled (Nelson 1997). There are many records of fully-grown fledglings grounded in forests and elsewhere, which were en route to the sea (Carter and Sealy

1987b, Burger 1994, Nelson and Hamer 1995, Nelson 1997), but the proportion of fledglings lost in this way is not known. Nelson and Wilson (1999) documented the death of a nestling from renal failure (dehydration), possibly due to being provisioned by only one parent. Another nestling died of a burst aorta (Nelson 1997).

3 DEMOGRAPHICS

3.1 Population characteristics

3.1.1 Sex ratio

Vanderkist et al. (1999) reported a significant male bias (1.8:1) among murrelets caught in floating mist nets in Desolation Sound, but concluded that this was likely due to behavioural differences between males and females. Subsequent radio-telemetry studies in this area confirmed that males made 1.3 times more visits to nests than females, and this difference was accentuated in evening visits and also towards the end of the chick-rearing period (Bradley et al. 2002). Birds caught or shot at sea show equal proportions of males and females (Sealy 1975a,b, Carter and Sealy 1984, Vanderkist et al. 1999), and a 1:1 sex ratio is assumed in population models (Beissinger 1995a, Beissinger and Nur 1997, Boulanger et al. 1999). Recently-fledged juveniles caught in Desolation Sound also have an equal sex ratio (Vanderkist et al. 1999; F. Cooke, unpubl. data).

3.1.2 Age at breeding

The average age of first breeding is not known, but based on other alcids of similar size is assumed to be between 2-5 years, with 3 years as a likely average (DeSanto and Nelson 1995, Beissinger and Nur 1997, Boulanger et al. 1999). Ricklefs (2000) showed that age of maturity was strongly correlated with annual adult mortality in birds, and applying the likely values of mortality (see section 3.1.7 below), his regression suggests maturity for Marbled Murrelets at 2-5 years (3 years if mean adult mortality is 0.15).

A bird identified on plumage characteristics as a sub-adult (i.e. 1-year old) was banded in Desolation Sound and when recaptured a year later had an underdeveloped brood patch, indicating possible breeding (F. Cooke and N. Parker, unpubl. data). Two juveniles recaptured a year later showed no signs of brood patch development. Although these data are inadequate to provide a mean age of first breeding, they do suggest that breeding might commence in some 2-year old birds. Preliminary analysis of plumage characteristics, inland flight patterns and size of the Bursa of Fabricius suggests that few second-year murrelets are likely to breed and most first breeding attempts occur at age three years or older (Thompson et al. 2002, pers. comm.). For their demographic model, Cam et al. (in review) considered that the proportion of birds aged 2, 3, 4, and 5 years which attempted to breed was 0.05, 0.40, 0.60, and 0.80, respectively.

3.1.3 Fecundity and breeding success

Fecundity in birds is generally defined as the annual number of female offspring which reach independence (fledge) per female of breeding age, including any attempts to re-lay after losing a

clutch. For most seabirds, this is measured at the time that the chicks leave the nest, and is derived from observations at nest sites. *Nesting success* is usually given as the number of fledglings per pair of adults that attempted breeding. Fecundity is therefore nesting success divided by two (considering only the female offspring and assuming a 1:1 sex ratio at fledging) plus an adjustment for the proportion of birds of breeding age which actually begin nesting.

Fecundity for Marbled Murrelets has also been defined differently, as the number of female offspring which reach the ocean per year per female of breeding age (Beissinger and Nur 1997), and fecundity is commonly estimated from counts at sea as the ratio between newly fledged juveniles and birds in adult plumage (see section 3.1.6). This at-sea measure of fecundity does not take into account loss of fledglings *en route* from the nest to sea, and therefore underestimates true fecundity (This and other sources of error are discussed in section 3.1.5). Accordingly, a distinction was made between *nest fecundity*, measured at the point of the fledgling's departure from the nest and comparable with data from most other seabirds, and *at-sea fecundity*, measured at the time the fledgling arrives at sea, and comparable with the juvenile:adult ratios commonly reported for Marbled Murrelets.

Marbled Murrelets lay a single egg per clutch (Sealy 1974), and some females lay a replacement egg following early breeding failure (see next section). It seems highly unlikely that a pair could raise two successive chicks per season. Maximum nesting success per season is thus 1.0 and maximum fecundity (at the nest or at sea) is 0.5.

3.1.4 Deriving fecundity from nesting success

To convert nesting success to at-sea fecundity (both terms defined in the previous section), one needs to divide nesting success by two (to get female fledglings per adult female). Additional adjustments (details discussed below) are needed to account for:

- the proportion of adult females that breeds each year (estimates range from 0.65 to 0.95);
- the proportion of fledglings that reach the sea after leaving the nest (estimated as 0.95);
- the number of nesting attempts per pair in each season, taking into account replacement laying (estimated to be 1.05, i.e., 5% replacement);.

These factors account for some of the discrepancies between observed breeding success measured at nest sites and juvenile:adult ratios measured at sea (discussed further below).

Adult seabirds in relatively predictable temperate environments usually attempt breeding each year (Nur and Sydeman 1999). The proportion of adult female Marbled Murrelets that breeds each year was assumed to be 0.9 by Beissinger and Nur (1997), based on comparative data from other alcids. Between 17 April and 6 July, when egg production occurred, 46-80% (mean 55%) of females captured in Desolation Sound in 2 years showed raised vitellogenin levels indicating egg production, but this sample included an unknown portion of immature females (McFarlane Tranquilla 2001). Based on telemetry data collected from 160 birds with known breeding status at Desolation Sound, a minimum of 62.5% of adults initiated a breeding attempt (Bradley 2002, Cam et al., in review). The proportion of immature individuals in this sample was unknown, and in some birds failure to breed was probably due to capture and handling stress (McFarlane

Tranquilla 2001). Cam et al. (in review) opted not to rely on physiology data because it was impossible to tell whether a "nonbreeder" classified using physiology was a bird skipping a breeding opportunity or a prebreeder. The distinction was required for the population matrix model. Taking these factors into account, Cam et al. (in review) used two proportions of adult females breeding each year in their demographic modeling: 0.80 and 0.95.

The proportion of pairs which re-lay following early failure is not known but there is evidence from telemetry studies and measures of vitellogenin (McFarlane Tranquilla 2001; R. Bradley and F. Cooke, unpubl. data) that a few pairs might re-lay within the same season. Studies in Alaska also indicate a low frequency of re-nesting, based on circumstantial evidence at one nest (Naslund et al. 1995), and the pattern of juvenile appearances at Naked Island (Kuletz and Kendall 1998). The prolonged breeding season in BC (late-April through early September; McFarlane Tranquilla 2001, Lougheed et al. 2002a), relative to the minimum time needed for incubation and chick-rearing (60-70 days; Nelson 1997), also suggests that some replacement laying occurs. Beissinger and Nur (1997) assumed there was no replacement laying (1.0 attempts per pair in each season), but the evidence suggests some re-laying occurs. A conservative guess of 1.05 attempts per pair per season was applied, i.e. 5% of lost eggs are replaced in the same season.

The difference between nest fecundity and at-sea fecundity is due to those fledglings which are "grounded" en route (Carter and Sealy 1987b) and presumably do not survive. The proportion of fledglings which reach the sea is unknown but Beissinger and Nur (1997) guessed that it was 0.9 for their model. This seems rather low and a value of 0.95 seems more appropriate, but is also just a guess.

3.1.5 Estimates of nesting success and fecundity

The most recent compilation of observations from nest sites across the Pacific Northwest showed nesting success as 0.35 fledglings per nest (n = 77 nests; Manley and Nelson 1999). Most of these nests were in BC and Oregon. Three measures of fecundity, derived from three different methods, are available from the Sunshine Coast, BC (including Desolation Sound) for the period 1994-2000, and are compared here (Manley 1999, Lougheed 2000, Cam et al., in review).

Manley (1999) observed 68 nesting attempts, using ground observations and tree climbing, and reported nest success as 0.33 fledglings per nest. If we apply the adjustments discussed above (considering females only; x0.95 to get proportion active breeders; x1.05 attempts per pair), this gives nest fecundity as 0.17 female offspring per adult female for this sample. If we assume that 95% of fledglings reach the sea then the at-sea fecundity would be 0.16 female offspring per adult female.

Based on the behaviour of 215 radio-tagged murrelets during incubation, coupled with observations at a sample of nests used by these birds to confirm fledging, nesting success in Desolation Sound was estimated to be 0.46 (Bradley 2002, Cam et al., in review). Applying the same adjustments as before, gives estimates of nest and at-sea fecundity of 0.23, and 0.22 female

offspring per adult female, respectively. The proportion of radio-tagged murrelets whose breeding attempts failed but which continued to fly inland regularly in the same manner as successful breeders is not known (Bradley 2002). Among other alcids some adults continue to visit nesting areas after losing an egg or chick (Gaston and Nettleship 1981, Wanless and Harris 1986), but this behaviour might be less common among Marbled Murrelets that are evidently not defending a specific nest site and it is premature to make adjustments for this behaviour. In California non-nesting murrelets continued to make regular inland flights, in one case up to two weeks after the fledging period (Green et al. 2002). The telemetry method may also miss very early failures, because some consistent movement pattern is needed to identify and locate breeders. Those that fail very soon after laying might not be detected (Bradley 2002). On the other hand, capture effects and the difficulties of accessing nests to confirm breeding might contribute to underestimates of nest success (Bradley 2002).

For Desolation Sound and the Sunshine Coast, at-sea fecundity estimates based on nest observations therefore ranged from 0.16 to 0.22. These values are slightly higher than the adjusted ratio of juveniles to After-hatching-Year (AHY) birds (0.13) measured at sea in the same area (Lougheed et al. 2002b). This is discussed in more detail in the next section.

3.1.6 HY:AHY ratios as estimates of at-sea fecundity

The most common estimates of fecundity in Marbled Murrelet are based on counts made at sea of juveniles (HY = hatching year birds) relative to other birds (AHY = after hatching year, which includes adults and subadults >1 year old). The ratio of HY:AHY is also known as the *productivity index* (Kuletz and Kendall 1998). For the following reasons, comparisons of HY and AHY birds are likely to contain systematic errors and the productivity index needs adjustments to be reliably used as a measure of at-sea fecundity (Kuletz and Kendall 1998, Kuletz and Piatt 1999, Lougheed 2000, Lougheed et al. 2002b):

- juveniles viewed from a boat cannot be reliably separated from AHY which are moulting or in winter plumage, and since moult in AHY begins before fledging is over, the number of fledglings produced in the last part of the breeding season cannot be counted, although adjustments can be made to account for this problem (Lougheed et al. 2002b);
- juveniles emigrate away from the marine areas to which they fledge (Lougheed et al. 2002b found that the daily probability of birds remaining within her survey area was 0.829 for HY and 0.946 for AHY birds, giving mean residence times of 5.3 and 126 days, respectively);
- in many areas adults also emigrate after breeding and their numbers might decline precipitously at the time that late fledging is still occurring (Burger 1995a, Kuletz and Kendall 1998);
- the proportions of breeding adults among the AHY birds is usually not known, and large numbers of non-breeding or failed AHY attracted to good foraging sites would inflate counts of AHY birds and hence artificially lower estimates of local fecundity;
- the distribution of HY and AHY birds in various marine habitats often differs markedly within and among study areas (Kuletz and Piatt 1999), which might skew HY:AHY ratios if all habitats are not equally sampled;

• there might be differences in the detectability of individuals in different age-classes, based on differences in dive times, social interactions and other behavioural effects (e.g., juveniles appear to frequent kelp beds, where they are hard to see, more than do adults).

For the first four reasons, concurrent ratios of HY:AHY birds are likely to underestimate at-sea fecundity if juvenile emigration is high (as in Desolation Sound; Lougheed et al. 2002b) or numbers of non-breeding AHY birds are high, but overestimate fecundity if adult emigration is high and counts are made late in the breeding season (Kuletz and Kendall 1998). To adjust for some of these factors, Kuletz and Kendall (1998) proposed doing a series of sequential surveys and comparing counts of HY made during the fledging period with counts of AHY made during incubation. Lougheed et al. (2002b) were able to combine data from boat surveys and tracking of radio-tagged HY and AHY birds to make adjustments for these sources of error, particularly the rapid emigration of HY birds in Desolation Sound. Their adjusted productivity index (0.13) was considerably higher than the index derived from unadjusted concurrent counts (0.04). Their adjusted index compares favorably with the estimates of at-sea fecundity derived from nest observations (Manley 1999) and telemetry (Bradley 2002) in the same area (range 0.16-0.22; see previous section).

Beissinger and Nur (1997) used concurrent HY:AHY ratios rather than adjusted ratios as estimates of fecundity in their population model, which partially accounts for the low population growth predicted from their model (discussed below). To some extent, concurrent data taken from large study areas (e.g. Strong et al. 1995) will reduce the effects of local movements of HY and AHY birds, because fewer birds will move into or out a large study area than a small one during the fledging period. Our knowledge of long-range migration is, however, too rudimentary to correct for such long-distant movements at the time of fledging.

Unadjusted and concurrent counts of HY and AHY birds, although poor measures of true fecundity, are still useful for tracking annual variations and monitoring changes affecting the terrestrial or marine habitats of the murrelets. Obviously, as shown by Lougheed et al. (2002b), knowledge of local movements and marine distribution of both age classes within a study area will greatly improve the interpretation and reliability of the data.

3.1.7 Survivorship

The only data on survivorship in this species come from birds banded and recaptured in Desolation Sound, using mist-nets and dip-nets (Cooke 1999, Hull 2000). The most recent estimates (Cam et al., in review), including data from 1991-2000, indicate a mean annual adult survival of 0.83 (95% C.I. 0.72-0.90; effective sample size 1499 birds) for combined data from murrelets caught in dip-nets and mist-nets in two locations 6 km apart. A higher survival of 0.92 (95% C.I. 0.63-0.99) was calculated from birds caught in mist-nets only (Cam et al. in review). The mist-net sample seemed to include a higher proportion of breeders than in the combined mist-net and dip-net sample. The difference in survival between the two samples might therefore reflect differences in dispersal patterns (a higher probability of return in the mist net sample) and in the proportions of immature birds with lower survival rates (fewer in the mist-net sample). There was no apparent effect of radio attachment on survival (E. Cam, unpublished data). These

estimates are of *local* survival within the study area, and include possible permanent emigration, and also possible effects related to capture and radio-tagging. *True* survival, defined as the survival of birds from one year to the next and excluding migration effects, is not presently estimable in Marbled Murrelets but is likely to be higher (Cam et al., in review). Accurately estimating rates of immigration and emigration is difficult in colonial seabirds (Hudson 1985, Nur and Sydeman 1999), but for the non-colonial Marbled Murrelet it is an even more daunting obstacle.

Local survival of adult Marbled Murrelets, at least for the Desolation Sound population, is similar to that estimated from comparisons with other alcids. A multiple regression of body mass and reproductive rate from other alcids predicted annual survival as 0.85 (95% C.I. 0.81-0.88) for Marbled Murrelets (Beissinger and Nur 1997), and an earlier estimate based on body mass alone was 0.83 (DeSanto and Nelson 1995). Among alcids, adult survivorship ranges from 0.75-0.77 for small species, similar in mass to Marbled Murrelets, to 0.91-0.94 for large-bodied puffins and murres (DeSanto and Nelson 1995). Beissinger (1995a) suggested that annual survival of Marbled Murrelets was expected to be high for their size class, but might be affected by predation of adults at inland nest sites. Population growth models for Marbled Murrelets are sensitive to variations in adult survival (Boulanger et al. 1999, Cam et al., in review), suggesting that populations are vulnerable to factors which impact adult survival, such as gill nets, oil spills and predation of adults.

Survival is strongly age-dependent in seabirds, being considerably lower in juvenile and subadult birds than in adults (Nur and Sydeman 1999). Little is known about the survival of immature murrelets. Banding of newly-fledged juveniles in Desolation Sound will ultimately yield estimates of their survival, but there are insufficient data to do this at present (N. Parker and E. Cam, pers. comm.). Beissinger (1995a), followed by Beissinger and Nur (1997) and Boulanger et al. (1999) estimated survival of first-year juveniles (age 0-1 years) and second-year subadults (1-2 years) based on the proportions of adult survival found in these age classes in other alcids. Juvenile and subadult survival rates were estimated to be 70.1% and 88.8% of adult survival, respectively. Cam et al. (in review) applied the same technique, but only for juveniles.

Survivorship curves, predicted from the Desolation Sound field data (Cam et al., in review) and from the estimates used by Beissinger and Nur (1997) are shown in Figure 3.1, assuming no effects of senescence. The low estimate of adult survival from Desolation Sound and the allometric estimate of Beissinger and Nur (1997) yield similar results, but the high estimate from Desolation Sound shows much greater longevity. For example, the percentage of fledglings alive at the start of their third year, when many might begin breeding, was 43%, 45% and 53%, respectively, and the percentage still alive at age 40 was <0.1% for the first two estimates, but 2.2% for the high Desolation Sound estimate.

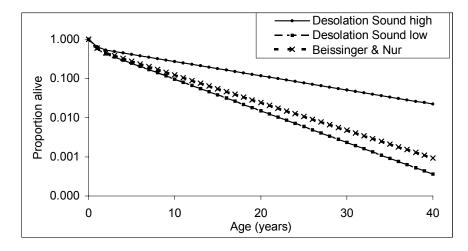


Figure 3.1. Survivorship curves predicted for Marbled Murrelets. Three measures of adult survival were used: high (0.92) and low (0.83) estimates from Desolation Sound (Cam et al., in review), and an estimate derived allometrically from other alcids (0.85; Beissinger and Nur 1997). In each case juvenile and immature survival was estimated to be 70.1% and 88.8%, respectively, of adult survival (Beissinger and Nur 1997). The y-axis is plotted on a logarithmic scale.

Banding and recapturing studies have not been in place for long enough to determine actual longevity. Cooke (1999) reported that two adults caught in 1991 were at least eight years old when recaptured in 1997.

3.1.8 Generation time

Surprisingly, there appear to be no published estimates of generation time for Marbled Murrelets. This parameter is important within the COSEWIC process where trends in populations are assessed relative to generation time.

Population parameters were applied to a simple life table to estimate generation time (Begon et al. 1990:148). Generation time depends on the age of first breeding and survival, but not fecundity. To cover the uncertainty in most of the parameters, a range of likely values was applied (Table 3.1). Five measures of annual adult survivorship were applied to cover the range of observed and possible values. Two values for average age at first breeding were considered: 2 and 3 years.

Table 3.1. Estimated generation time (years) based on life-table calculations using variable values of adult survival and mean age of first breeding.

		<u> </u>			
	Mean age at first breeding (years)				
Annual adult survival	2	3			
0.83	6.9	7.9			
0.85	7.6	8.6			
0.88	9.1	10.0			
0.90	10.4	11.3			
0.92	11.9	12.8			

The estimated generation time ranged between 6.9 and 12.8 years for the parameters considered. Until there are further data to refine these estimates it seems best to use a mean generation time of 10 years, which reflects a fairly optimistic estimate of adult survival, and a fairly conservative estimate of mean age of first breeding.

3.1.9 Age class structure and proportion of breeders:non-breeders

The life table used to estimate the survivorship curves and generation time shown above can also be used to estimate the age class structure (Table 3.2). This assumes no variation in breeding success or age-specific survival through the life of a cohort. i.e., constant conditions over many years.

Table 3.2. Proportions of subadults and adults at the start of the breeding season predicted by applying the estimated juvenile and immature survival (70.1% and 88.8% of adult survival, respectively) to the measures of adult survival from Desolation Sound (high estimate 0.92; low 0.83; Cam et al., in review) and that estimated by Beissinger and Nur (1997).

	Mean age of first breeding (ye			
Data source for adult survival	2	3		
Desolation Sound high				
Subadults	0.09	0.17		
Adults	0.91	0.83		
Desolation Sound low				
Subadults	0.19	0.33		
Adults	0.81	0.67		
Beissinger & Nur (1997)				
Subadults	0.17	0.29		
Adults	0.83	0.71		

Sealy (1975b) found that 15% of the population sampled through the breeding season (late April through late August) near Langara Island, BC, were immature on the basis of smaller bill and wing dimensions, lack of brood patch and undeveloped gonads, although their plumage was similar to that of adults. Sealy (1975b) assumed that these immature birds were yearlings and two-year olds, but it is possible that he was distinguishing only yearlings, given their smaller size, and recent work that suggests some two-year olds might attempt breeding (F. Cooke, unpubl. data).

The Desolation Sound study provides some information on the proportion of active breeders. McFarlane-Tranquilla (2001) found that 55% of captured females (range 38-87%) had raised vitellogenin levels indicating egg production, during the period when egg-production was expected. Based on the behaviour of radio-tagged birds making repeated inland trips, the proportion of active breeders in the Desolation Sound telemetry sample was estimated to be 62.5% (Bradley 2002), but this is a minimum estimate because some birds might have postponed

breeding as a result of capture and handling (McFarlane-Tranquilla 2001), and some birds which failed early in incubation might not have been detected by these methods.

Several factors make it extremely difficult to estimate accurately the proportions of breeders and non-breeders in a population of Marbled Murrelets. Immature birds might not arrive at breeding areas at the same time as adults (Carter 1984) and hence be under-represented in the captured sample. Breeders and non-breeders might not forage in the same areas and hence capture sites might provide different results. Immature females might have elevated vitellogenin but not lay an egg, and conversely the prolonged breeding period of the murrelets makes it likely that some late breeders or females that lay replacement eggs are not identified. The age of first breeding is not known. In most seabird species there are mature birds that do not breed in every year, and this probably occurs among Marbled Murrelets too, which would elevate the proportion of non-breeders.

In summary, there is a range of estimates from various sources of the proportion of breeding adults in murrelet populations. Even defining active breeding is difficult and different measures have been used in various analyses. Dissection of shot birds off Langara Island suggests 85% (Sealy 1975b). Behaviour, brood patch state and vitellogenin measures from Desolation Sound indicate 55-95%. Models derived from life-history data and correlations with other alcids suggest 67-91%, depending on the estimate of adult survival and age of first breeding (Table 3.2). The age structure and proportion of adults actively breeding is likely to vary among study sites, among years, and even within seasons (if adults and immatures follow different movement patterns).

3.1.10 Productivity and population growth

Population dynamics of Marbled Murrelets were modeled from demographic data by Beissinger (1995a; updated in Beissinger and Nur 1997) and Boulanger et al. (1999). The goals of the models were to determine whether current estimates of survival, fecundity and age at first breeding yielded stable, increasing or declining populations. Conversely the models also explored the range of demographic values required to maintain stable populations. Neither model incorporated the recent demographic data from the Desolation Sound study (Cooke 1999, Cam et al. in review), refined application of HY:AHY ratios (Kuletz and Kendall 1998, Lougheed et al. 2002b), or larger samples of breeding success resulting from nest observations (Manley 1999, Manley and Nelson 1999, Cooke et al. unpubl. data). Cam et al. (in review) combined demographic parameters measured in the long-term capture-mark-recapture and radio-telemetry study in Desolation Sound to model the likely population growth in this population. These studies are reviewed here.

An important product of these demographic models is the population growth parameter lambda (λ) . This is a measure of the annual rate of population growth, derived from demographic parameters such as age-specific survival and fecundity, age of first breeding, proportion of adults breeding etc. If $\lambda = 1$ the population is stable, if $\lambda < 1$ the population is declining, and if $\lambda > 1$ the population is increasing.

Beissinger and Nur (1997) based their population model on measured and estimated population parameters from across the Pacific Northwest. They used fecundity estimates based on observations at nests (mean fecundity 0.146) and concurrent HY:AHY ratios from at-sea counts made in Washington, Oregon and California (range 0.01-0.14, but 0.04-0.14 in more productive areas likely to be typical of BC). As discussed above these now appear to be underestimates of fecundity. Adult survivorship was estimated to be 0.85 based on equations using data from other alcids, as explained above. They modeled the range of demographic parameters (adult survivorship, fecundity and age of first breeding) which would produce a stable population, neither increasing nor decreasing (i.e., $\lambda = 1$) (Figure 3.2).

Beissinger and Nur (1997) plotted all the likely values of fecundity (range 0.06-0.18) and survivorship (0.85-0.90) available to them, which fell in the rectangle shown as MM in Figure 3.2. These values always fell below the lines where $\lambda = 1$ regardless of age of first breeding, indicating that populations were declining. They concluded that reproductive success throughout the Pacific Northwest was insufficient to sustain murrelet populations, which were likely to be declining at least 2-4% per year, and conceivably even 2-3 times faster than this. Beissinger and Nur (1997) also considered the demographic parameters which would yield a stable population ($\lambda = 1$). For the range of adult survival they considered most likely (0.85-0.90), fecundity would have to range from 0.20-0.46.

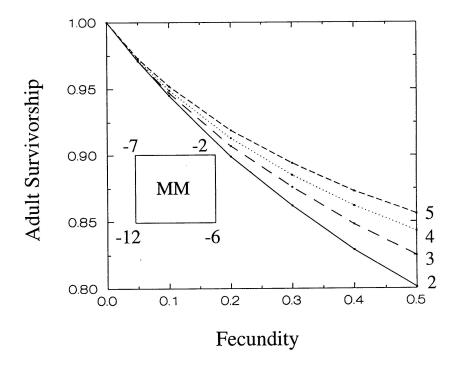


Figure 3.2. Output from the population model by Beissinger and Nur (1997). The lines show isobars where lambda λ equals 1 (i.e., populations are neither increasing or decreasing) for different combinations of fecundity and annual survivorship. Above the isobars populations should increase and below the isobars populations should decline. Lines are shown for ages of first breeding from 2 to 5 years. Likely values of annual survivorship and fecundity for Marbled

Murrelets are given by the box labeled MM. Average annual adult survival is expected to fall between 0.85 and 0.90 based on comparisons with other alcids. Maximum fecundity was set by uncorrected nesting success (fecundity 0.18 or nesting success of 0.36) and minimum fecundity from low at-sea juvenile:adult ratios (0.06). All likely values of reproduction and fecundity for the Marbled Murrelet (MM) fall within the rectangle and indicate declining populations. The annual percentage decline for each corner of the rectangle is shown. Note that this analysis did not include the more optimistic data now available from Desolation Sound (Cam et al. in review.).

Cam et al. (in review) were able to draw upon more comprehensive demographic data derived from their field work in Desolation Sound, BC. This is the only field study to date which is able to provide measures of both adult survival and fecundity. Some parameters remain unknown or uncertain, including the age of first breeding, survival of juveniles and sub-adults, and the proportion of adults breeding each year. Cam et al. (in review) assumed that a small proportion of murrelets began to breed in their second year (0.05) and that this proportion progressively increased to 0.80 at year six (see section 3.1.2). They modeled two estimates of the proportions of adults breeding in each season: 0.80 and 0.95 (see section 3.1.9). They assumed that the annual survival of juveniles was 0.58 (70.1% of adult survival), and modeled two estimates of adult survival: 0.83 measured in the combined mist-net and dip-net sample, and 0.92 measured in the mist-net sample only (see section 3.1.7). Population growth rates (λ) produced by these models ranged from 0.915 (declining population, with relatively low adult survival) to 1.02 (increasing population, with higher adult survival; Table 3.3). The model was more sensitive to the estimates of adult survival used than to estimates of the proportion of adults breeding. Adult survival has to be 0.90 or 0.91 for this population to be stable (Cam et al., in review). As explained by Cam et al. (in review) the estimates of adult survival might be underestimates because they include some unknown effects of emigration.

Table 3.3. Estimates of population growth rates (lambda) based on demographic parameters from Desolation Sound, BC (Cam et al., in review).

Proportion of adults breeding	Annual adult survival	Population growth rate (lambda)	"Confidence interval" for lambda*
0.95	0.83	0.925	0.82-1.02
0.80	0.83	0.925	0.81-1.01
0.95	0.92	1.02	0.88-1.16
0.80	0.92	1.01	0.87-1.15

^{*}The confidence interval was calculated using variances of parameters measured in the field (breeding success and adult survival) and does not therefore cover the uncertainty in all the input parameters (see Cam et al., in review).

The Desolation Sound data suggest that the conditions required for stable, or slowly increasing populations ($\lambda \le 1$) are possible, if reasonably optimistic estimates of adult survival and fecundity are assumed. The parameters used by earlier models (Beissinger and Nur 1997, Boulanger et al. 1999) might be too pessimistic, at least for the Desolation Sound population. There are unfortunately no other studies in other areas which might provide comparative

demographic data. Given the high cost of the multi-year mark-recapture and telemetry studies required, it seems unlikely that there will soon be a comparable range of data from outside Desolation Sound. Smaller-scale studies, however, could contribute valuable measures of adult survival (from mark-recapture studies) and fecundity (from observations at nests, or at-sea counts of fledglings) to improve and confirm demographic models. Demographic parameters in seabirds can vary substantially among years and across a species' range (Hudson 1985, Nur and Sydeman 1999), and Cam et al. (in review) caution that generalizations based on a single location might be risky.

Detecting significant changes in populations might be difficult using current at-sea monitoring. On the basis of their population model, Boulanger et al. (1999) predicted that only large changes in demographic parameters (e.g., 20% reduction in adult survival or >50% reduction in fecundity) would be detectable within 10 years using current survey methods. Becker et al. (1997) concluded that they should detect population changes of 9% over 10 years with an estimated power of 80% based on line transects (Distance sampling method) repeated 5 times per season. With relatively high densities of murrelets in Alaska, Kuletz and Kendall (1998) reported that their power to detect a 50% change in juvenile abundance was generally >80% within 10 years with 5 surveys per year, or within 5 years with 8 surveys per year. For AHY birds, power was 80% to detect changes of 30% over 5 or 10 years, with 5 surveys per year. Preliminary analysis of adult densities, juvenile densities and juvenile:adult ratios from multi-year at-sea surveys in Prince William Sound, Alaska shows that far fewer surveys are needed to detect differences among study sites, than to detect changes among years at these sites, but details are not yet available (K. Kuletz, pers. comm.).

3.1.11 Critical stages of the life cycle impacting population dynamics

Boulanger et al. (1999) and Cam et al. (in review) found that population growth in Marbled Murrelets was most strongly influenced by changes in adult survival, followed by juvenile survival and nesting success (productivity). Boulanger et al. (1999) expressed concern that gillness and oil-spills, which could impact adult survival, posed a threat to murrelet populations. These topic are discussed in more detail in section 6.2.

Even though demographic models consistently show that population growth is most sensitive to changes in adult survival, that does not necessarily mean that adult survival is currently limiting populations. The variability in age-specific survival or fecundity is not known. It is quite feasible that fecundity (breeding success) limits murrelet populations in many parts of their range. In most seabirds, adult survival is high and populations are usually limited by reproductive output, mediated through food supply or limited nest sites (Birkhead and Furness 1985, Croxall and Rothery 1991, Cairns 1992). Population models for the Spotted Owl (*Strix occidentalis*) show that population growth is most sensitive to adult survival (as in the murrelet models), but population decline can still be a product of low fecundity or immature survival, and management needs to address these factors (Seamans et al., 2001). Murrelet populations will decline if breeding habitat is lost, even if adult survival is unaffected.

Breeding success in Marbled Murrelet is likely to vary widely with time and space. In some years breeding success might fall well below the average, as occurs among other seabirds (Nur and Sydeman 1999), especially those affected by El Niño events (Ainley and Boekelheide 1990). There are indications, but no conclusive data, that Marbled Murrelets in BC might be negatively affected by warm ocean conditions (Burger 2000). Other alcids (Cassin's and Rhinoceros Auklets) are known to have reduced breeding success during warm ocean conditions in BC (Bertram et al. 2000, 2001). Ralph et al. (1995b) suggested that current demographic measures for murrelets might be low because they were collected in the 1990s when marine productivity in the Pacific Northwest was often negatively influenced by warm water events. Clearly, a longterm series of demographic measures which cover other climatic and ocean regimes are needed. Beginning in late 1999, the eastern North Pacific appeared to be entering into a "cool" phase in the Pacific Decadal Oscillation, and it will be interesting to see if there are changes in demographic parameters of Marbled Murrelet relative to the "warm" 1990s. Preliminary results from Desolation Sound indicate that nest success was higher in 2000 and 2001 than in the 1990s (F. Cooke, pers. comm.). If the population dynamics of murrelets are negatively affected by warm ocean conditions, this raises additional concerns about the likely long-term impacts of global climate change (see section 5.4).

3.2 Population size and distribution of Marbled Murrelets in British Columbia

3.2.1 Census data

The population of Marbled Murrelet breeding in BC is not known and is not likely to be accurately estimated for many years. There are simply too many areas in which there have been no attempts to count murrelets. Rodway (1990, also Rodway et al. 1992) estimated the BC population using at-sea counts, most from the 1970s and early 1980s, which covered only a small portion of the provincial coastline. Rodway estimated that the total population was between 45,000-50,000 breeding birds, and assumed that 85% of all birds counted in summer were breeding adults (Sealy 1975b), which gives a total summer population of 53,000-59,000 birds of all ages.

There are now considerably more data with which to derive an estimate of the provincial population, although very large parts of the range have no counts. The most current information on murrelet numbers from at-sea surveys, radar counts, and a few other methods was assembled in an attempt to estimate the provincial total. Some points to note about these data:

- Data were restricted to the breeding season (loosely taken as 1 May through 31 July), but in a few cases data that were within a week or so of these dates were accepted.
- Counts used were from the 1990s and 2000, unless earlier studies were more complete and reliable (e.g. Barkley Sound and parts of Moresby Island).
- All numbers presented are of all birds counted, which would include non-breeding subadults and for a few late summer counts, newly fledged juveniles. The proportion and number of breeding adults is estimated at the end of this section.

- Actual numbers counted in census studies are reported, but where authors have made some attempt to extrapolate their data to estimate the total population within the study area that is reported separately.
- In most cases the actual local population is likely to be higher than the numbers counted. Both at-sea surveys (Becker et al. 1997) and radar counts (Burger 1997a) underestimate the actual populations being sampled. In addition there were nearly always significant parts of the study areas which were not included in censusing. In some cases researchers made adjustments to their data to account for these underestimates and gaps, and such extrapolations are reported separately from the actual counts.
- Radar counts of birds entering watersheds or inlets were invariably higher than at-sea counts made in the same areas, and were given preference. In all radar counts, however, some forested areas where murrelets were likely to nest were not included.

Given the limitations of all census methods, the maximum actual counts were used as estimates of the minimum number of murrelets likely to be in each area, and in some areas the estimated populations based on extrapolations from these data are reported.

The at-sea and radar counts used in this analysis are given in Appendices 1 and 2, respectively, and explained in more detail in the next section. Two estimates of the total population per region are made: the "pessimistic" estimate uses the lowest likely counts taking into consideration the proportion of the area surveyed and the precision of the survey method; the "optimistic" estimate uses the highest likely count supported by the data in each region. These data indicate a provincial population between 54,700 (pessimistic) and 77,700 (optimistic) birds (Table 3.4; this method does not provide any confidence limits around these estimates). The median between pessimistic and optimistic estimates is about 66,000 birds. The limitations of these estimates are discussed below.

Table 3.4. Counts and estimated populations of Marbled Murrelets in British Columbia during the breeding season (May through July). See Appendices 1 and 2 for details.

Actual Pessimistic Optimistic estimate estimate Method Source Area counts Victoria Harbour to Port San Juan 200 300 Various Appendix 1 Owen Point to Cape Beale 2,859 3,000 3,300 At-sea Burger 1997b Barkley Sound 3,600 3,406 3,000 At-sea Sealy and Carter 1984 200 300 Vermeer & Morgan 1992 Alberni inlet 212 At-sea Clayoquot Sound and Long Beach 5,536 6,000 8,000 Radar Burger 2002 NW Vancouver Island 5,930 6,500 8,000 Radar Manley 2000 1,000 Appendix 1 NE Vancouver Island 418 500 At-sea Total West & North Vancouver Island 18,361 19,400 24,500 East Vancouver Island 437 700 1,000 At-sea See Appendix 1 Southern Mainland 2,437 6,000 7,000 Various See Appendix 2 & text Central Mainland 3,355 10,000 21,000 Radar See Appendix 2 & text Northern Mainland 1,859 10,128 14,662 Radar See Appendix 2 & text See Appendix 1 Queen Charlotte Islands/Haida Gwaii 6,063 8,500 9,500 At-sea 32,512 **Total for British Columbia** 54,728 77,662

3.2.2 Explanation of census data

The following notes explain the selection and treatment of data used to estimate the provincial population.

West and north coasts of Vancouver Island

Barkley Sound and Long Beach: Sealy and Carter's (1984) grid count in 1982 (3406 birds) remains the most complete census, although several transect counts repeated in the 1990s in Barkley Sound found fewer murrelets than in the early 1980s (Burger 2000). On the other hand the grid count likely missed a significant portion of birds (H. Carter, pers. comm.). Therefore, even with some decline there are still likely to be at least 3000 murrelets in Barkley Sound and optimistically 3600.

Clayoquot Sound and northwest Vancouver Island: Burger (2001, 2002) used the mean of the annual maximum count per watershed over three years to estimate the population entering 20 watersheds as 5536 birds. The highest at-sea count in Clayoquot Sound between 1992-1996 was 4510 birds (Kelson and Mather 1999). Taking into account areas not covered by the radar counts, Burger (2002) estimated the total Clayoquot Sound population to be 6000-8000 birds. Applying the same reasoning to northwest Vancouver Island, Manley's (2000, unpublished data) radar count of 5930 birds in 32 watersheds in 1999 and 2001 (Appendix 2) was taken to represent a population of about 6500-8000 murrelets for the region. Manley (2000) reported 1726 birds from 1062 km of at-sea transects in this area.

Northeast Vancouver Island: The Marbled Murrelet Recovery Team has decided to combine this area with the west coast of Vancouver Island for monitoring and management purposes, because of similarities in forest ecosystems. Apart from counts made in 1991 by Savard and Lemon (1992) which cover a small portion of the area, the murrelets here have not been counted. Their count of 418 birds suggests that there are at least 500 and possibly over 1000 murrelets in this area.

East Coast Vancouver Island (Victoria to Campbell River)

There have been very few recent surveys in this area, primarily because the population is regarded as small and depleted. Given the many gaps in coverage, the minimum count of 437 birds was estimated to represent a likely population of 700-1000 murrelets.

Southern Mainland

Sunshine Coast: Five different models of population based on recaptures of marked murrelets in mist nets at Theodosia Inlet gave estimates averaging 3748 murrelets (range 2541-4326; Drever et al. 1998), from which Lougheed et al. (1998) estimated the population for the greater Desolation Sound area to be about 5000 birds. Using a larger sample of these mark-recapture data (1994-2000), Cam et al. (in review) estimated the mean population to be 4374 birds (range 2431-7198). The low rate of recapture suggested that birds were drawn from a large area, and not just Desolation Sound alone, and this was confirmed by radio-telemetry (Bradley 2002). Multiple radar counts from 21 watersheds in the Sunshine Coast in 2000-2001 gave a total count of 2437

birds, using the mean of the annual maximum per watershed (Cullen 2002; see Appendix 2). At sea surveys in this study covering 946 km yielded 1251 murrelets (Cullen and Manley 2001).

Outside the Sunshine Coast: At sea surveys have covered only a portion of the area and yielded about 100 murrelets (Appendix 1). The population outside the Sunshine Coast is probably larger than this, and radar counts are planned for 2002.

Overall it seems probable that 6000-7000 murrelets occur in the entire Southern Mainland area in summer.

Central Mainland

Bute Inlet through north end of Princess Royal Channel: This area is covered by the Central Coast Land and Resource Management Plan (CCLRMP). There have been numerous at-sea surveys for portions of this large, complex coastline (see Burger 1995a), but two recent studies using radar provide better estimates of the populations (Drever and Kaiser 1999, Schroeder et al. 1999). Both studies sampled only a portion of the forested habitat available, but in both cases the authors made estimates of the larger regional population.

In 1998, Schroeder et al. (1999) completed radar counts at 22 watersheds within this area (excluding Bute Inlet) and also counted murrelets along boat transects. With radar they counted 3355 murrelets entering the 22 watersheds (Appendix 2). To estimate the total population of murrelets within the CCLRMP area, they calculated the density of murrelets per area of suitable habitat within these areas (defined slightly differently in five simulations) and then extrapolated the density to the total area of suitable habitat within the entire area. The estimates based on five different habitat models ranged from 5,343 to 42,359 murrelets, and they concluded that the most reasonable model was the one that estimated 21,352 murrelets. At-sea surveys done in the same study yielded 3,938 murrelets along 29 transects totaling 1300 km. The area is likely to support at least 10,000 murrelets (3x the actual radar count; Appendix 2).

Drever and Kaiser (1999) also did radar counts within the Central Mainland coast in 1998, but counted murrelets entering selected channels, bays and inlets, rather than at selected watersheds as Schroeder et al. (1999) did. Drever and Kaiser (1999) counted 6268 murrelets at 21 stations, but some of the birds were evidently counted at more than one station as they flew up the channels or inlets. They estimated that 2221 murrelets entered the watersheds above nine inlets, and made a rough estimate that this represented 5442 murrelets within the study area (which did not cover the complete CCLRMP area).

Northern Mainland

Laredo Sound to the Alaska border (excluding Princess Royal Island): This remains the most poorly sampled part of the BC coast. Kaiser et al. (1991) and J. Kelson (unpublished) provide the only at-sea counts, covering only a small portion of the coast (Appendix 1). These data indicate that murrelet densities at sea appear lower than along the Central Mainland coast. Preliminary analysis of radar counts made in 2001 (D. Steventon and N. Holmes 2002) gave a total count of 1065-1859 murrelets entering 26 watersheds (Appendix 2). Extrapolating from these data using a Habitat Suitability Index model to weight habitat quality and area, D.

Steventon (unpubl. data) estimated that the total population for the Northern Mainland (North Coast and Kalum Forest Districts) was 10,128 murrelets, if a pessimistic density was applied, or 14,662 murrelets, if an optimistic density was used (Appendix 2).

Queen Charlotte Islands/Haida Gwaii

There have been numerous at-sea surveys of murrelets in this archipelago, but much of the data comes from 25 or more years ago, and large parts of the coast have not been adequately surveyed. The following notes explain the major sources of data.

Lyell Island, Darwin Sound and Juan Perez Sound: French (1993) extrapolated habitat-specific densities to estimate a total population of murrelets of 2550 in 1992. Lawrence and Backhouse (1991) estimated 2655 birds in south Juan Perez Sound alone in 1991. French (1993) reported 52% of all murrelets in 1992 were in south Juan Perez Sound. Overall it seems that the likely population for this area was at least 2600 and perhaps as high as 5000 birds in 1991-1992.

Skincuttle Inlet, Poole Inlet and Collison Bay: Lawrence and Backhouse (1991) estimated 1161 murrelets by extrapolating habitat-specific densities measured on at-sea surveys.

Skidegate Inlet and Channel, and south coast of Graham Island: Rodway et al. (1991) reported numerous boat transects and telescope counts, which often overlapped spatially. In most cases the counts did not cover the entire area and the numbers reported here are therefore likely to be minimum estimates (Appendix 1).

North coast of Graham Island: Again Rodway et al. (1991) give details on several boat counts, but these did not cover the entire coast so are likely minimum counts. The count of 612 murrelets reported between Pillar Bay and Masset Sound on 15 July 1989 by Rodway et al. (1991, page 57), and repeated in another report (Anon. 1994), needs confirmation (M. Rodway, pers. comm.), because in Appendix 17 of Rodway et al. (1991) these data are reported as counts of 6, 1, and 2, totaling 9 birds. Sealy (1975a) stated that most Marbled Murrelets on this coast foraged in Pillar Bay and in Cloak Bay (Langara Island), and his counts for the latter area from 1971 were included.

West coast of Graham Island: The available data are patchy, often more than 25-years old, and do not cover the entire coast. The surveys made by Vermeer et al. (1983) were often made further offshore than the areas frequented by most Marbled Murrelets. Additional surveys made in parts of this coast by D. Hatler et al. (unpubl. data provided by A. Harfenist) and others (Appendix 1) probably overlap somewhat with Vermeer's samples, but appeared to cover more inshore waters than Vermeer et al. and were therefore added to the Vermeer et al. total. Overall, the counts almost certainly underestimate the population in this area, and adequate censusing, ideally using radar, is urgently needed.

Overall, the Queen Charlotte Islands/Haida Gwaii population appears to be at least 8,500 birds and is likely about 9,500 if the areas not surveyed are considered.

3.2.3 Comments on the estimated British Columbia population

There were over 32,000 Marbled Murrelets actually counted in at-sea and radar counts in BC, with most counts made in the late 1990s or 2000. These counts would be affected by seasonal variations, movements among areas, and local population demographics, but it seems certain that the provincial population is considerably larger than this, given the very incomplete coverage of the coast and the fact that most counts underestimated the number of birds even in areas surveyed. Estimates of regional populations based on these counts give totals of 54,700-77,700 (median 66,000) murrelets. There is much less certainty around these estimates and the actual number might be either higher or lower than this. The total population might be higher if counts in areas poorly sampled have large populations, and might be as high as 80,000 birds. On the other hand, the extrapolation models used in some areas might overestimate populations.

A population of 66,000 birds would likely include about 56,000 breeding birds (using Sealy's 1975b measure of 85% breeding birds), which is slightly higher than Rodway's (1990) original estimate of 45,000-50,000 breeding birds. The difference between Rodway's estimate and the current one does not indicate any change in population size since 1990. There are no data that show population increases from 1990-2001 in BC. The differences simply reflect increased efforts and better methods for counting murrelets in BC.

Population estimates from the Central and Northern Mainland and the Queen Charlotte Islands are probably the least reliable. In the two mainland regions the populations were estimated from a single year of radar counts extrapolated using correlates with areas of apparently suitable habitat. The numbers of murrelets per 1000 ha of suitable habitat varied considerably among the sampled watersheds, and the interpretation of suitable habitat from the GIS data also has scope for error. Additional research on habitat associations and greater sampling of watersheds will improve these estimates. In the Queen Charlotte Islands/Haida Gwaii the estimates are based on at-sea counts which cover variable portions of the coastline and probably underestimate the archipelago's population. Radar surveys have consistently produced higher counts of murrelets than at-sea surveys in the same areas.

Until better data are available it seems reasonable to estimate the British Columbia population to be 66,000 Marbled Murrelets, with the bulk of the population breeding on the west coast of Vancouver Island, the Central Mainland coast, Desolation Sound and adjacent areas on the Southern Mainland, Queen Charlotte Islands/Haida Gwaii and possibly the Northern Mainland.

3.3 Population trends in British Columbia

There is anecdotal evidence that populations of Marbled Murrelets in the Strait of Georgia declined significantly in the early 1900s. Brooks (1926) commented on the scarcity of Marbled Murrelets along the east coast of Vancouver Island in 1925-1926 compared with numbers observed in 1920 and earlier. Pearse (1946) reported a decline in numbers around Comox between 1917 and 1944, concomitant with the loss of large tracts of the surrounding coniferous forests.

Despite considerable inventory and research since 1990 it remains difficult to determine population trends for any region of BC for several reasons:

- there are very few data from standardized censuses from earlier years;
- most data show considerable seasonal and annual variations, making it difficult to determine long-term trends;
- populations are likely to change slowly in this long-lived bird, unless there is catastrophic mortality of adults, for which there is no evidence.

Rodway et al. (1992) found no clear trends in Christmas Bird Count data from 1957 through 1988. This analysis has not been expanded to include more recent data, because few count areas overlap with significant wintering populations in BC and Christmas Bird Count data seem to be poor indicators of widespread population trends in this species (Piatt 1998, Hayward and Iverson 1998).

The most obvious and widely-quoted evidence of population change in BC is the data from at-sea surveys made in Clayoquot Sound in 1982 (Sealy and Carter 1984) and repeated using the same method in 1992, 1993 and 1996 (Kelson et al. 1995, Kelson and Mather 1999). These data evidently show declines in populations of between 22% and 40% since 1982, attributed to the effects of logging (Kelson et al. 1995). Closer examination of these data, however, revealed that the only significant change occurred in the exposed inshore zone, and there was no evidence of change in the protected channels (Figure 3.3; Burger 2000). Furthermore, the total change and the change in the exposed inshore zone might be linked to warm sea temperatures, which were considerably higher in the 1990s than in 1982, and are associated with less suitable foraging conditions for murrelets on this coast (Burger 2000). There are insufficient data to statistically separate the effects of temperature and years, but clearly temperature effects need to be considered in examining local trends. A clearer picture might emerge if these counts are repeated in the next few years when sea temperatures are expected to be lower than in the 1980s and 1990s.

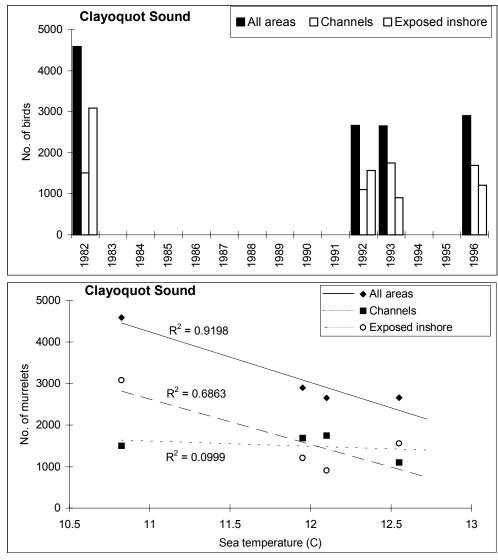


Figure 3.3. Counts of Marbled Murrelets in Clayoquot Sound, showing data from sheltered channels and exposed inshore areas, plotted against year (upper graph) and sea temperature (lower). From Burger (2000) using data from Sealy and Carter (1984), Kelson et al. (1995) and Kelson and Mather (1999).

A similar comparison uses counts made in Trevor Channel, Barkley Sound, BC, in 1980 (Carter 1984) and repeated annually from 1992-2000 (Figure 3.4). Here there was no apparent effect of sea temperature (r = 0.046, P = 0.899, N = 10) but there was a decline with years, which was not statistically significant (r = -0.539, P = 0.108, N = 10). None of the annual mean counts made since 1992 have been as high as in 1980.

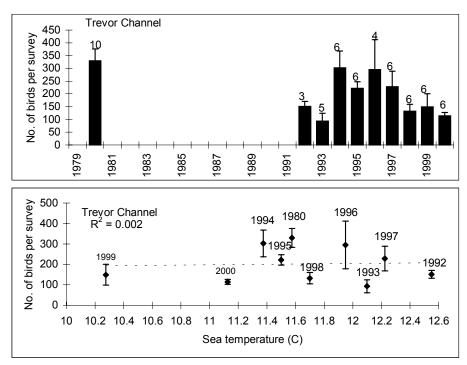


Figure 3.4. Mean (± SE) counts of Marbled Murrelets made in Trevor Channel, Barkley Sound between mid-May and mid-July. The upper graph shows the trend with years and the lower the counts in relation to sea surface temperatures (Burger 2000, Burger and Stewart, unpubl. data).

A separate transect in the same area, running from Trevor Channel past Cape Beale shows a decline in Marbled Murrelets since 1979, although not significant (Figure 3.5; r = -0.371, P = 0.468, N = 6), and these data were also not significantly correlated with sea temperature (Burger 2000; r = -0.621, P = 0.188, N = 6).

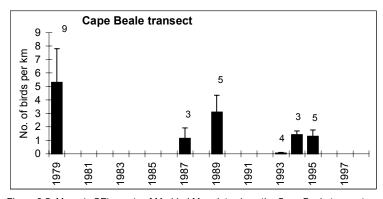


Figure 3.5. Mean (\pm SE) counts of Marbled Murrelets along the Cape Beale transect between mid-May and mid-June (from Burger 2000). Numbers of surveys in each year are shown above the columns.

Occupied detections from audio-visual surveys made at 11 stations in the Carmanah-Walbran from 1991 through 1999 showed a significant negative correlation with sea temperature (Burger 2000). A new analysis, using analysis of covariance (ANCOVA) with sea temperature as a covariant, shows a significant negative trend over the 9 years (Figure 3.6; adjusted $r^2 = 0.347$, P<0.001). Since 1990 there has been no logging in the Carmanah valley, but parts of upper

Carmanah were logged in the late 1980s and logging continued in the upper Walbran close to the observation stations. The slow but significant decline through the 1990s might be due to residual effects of these logging activities, but other causes might also be involved.

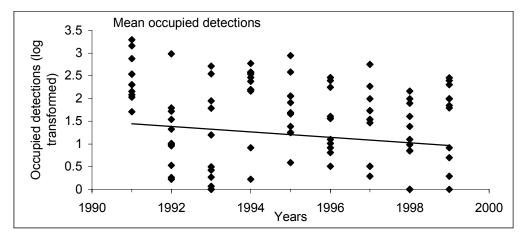


Figure 3.6. Trends in occupied detections of Marbled Murrelets in Carmanah-Walbran. Each point represents the mean frequency of occupied detections from 3 or more surveys at each station per year. The trend line was determined by the parameter estimates of the ANCOVA analysis (Burger and Bahn 2000).

Counts of birds along a 6 km stretch of shoreline at Boundary Bay, south of Vancouver, between November and August showed a decline from an average of 66 Marbled Murrelets in 1980-1981 to 2 in 1994-1995, and no birds in 1996 and 1997 (Cooke 1999). Murrelets appear to have disappeared from Burrard Inlet near Vancouver since 1990 (G. Kaiser quoted by Hull 1999). Cooke (1999) thought they had insufficient number of years to detect trends from the at-sea surveys in Desolation Sound.

In Queen Charlotte Islands/Haida Gwaii sparse data from the 1990s showed no consistent trends when compared with similar counts made by Vermeer et al. (1983) in 1977 (Burger 1995a). Boat surveys have been done annually since 1990 in and near Laskeek Bay (Gaston 1996). These followed 16 fixed transect routes (53.8 km in total), covering the range of marine habitats used locally by Marbled Murrelets. Data from 1990-1998 were available for analysis (Figure 3.7). These showed considerable variations within and among years but no significant trends over the years (r = -0.249, P = 0.518, N = 9). Exceptionally high counts were made in 1993, which coincided with exceptionally low counts off southwest Vancouver Island (see above), suggesting that there might be some long-range movement from the southern outer coast into Hecate Strait during El Niño years (Gaston 1996). This remains to be confirmed.

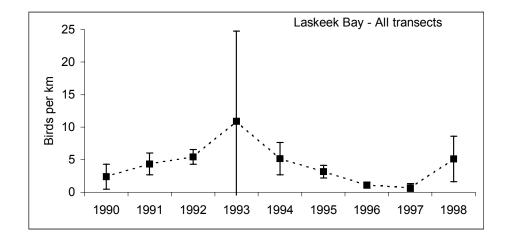


Figure 3.7. Mean (± SD) densities of Marbled Murrelets (birds per linear km) from boat transects made May and June in Laskeek Bay, Queen Charlotte Islands/Haida Gwaii. Surveys covered 4 days per year (12 in 1990), averaging 42.5 km per survey (range 10.5-53.8 km). Data from A.J. Gaston and Laskeek Bay Conservation Society.

Conclusions about population trends in BC - There are insufficient data to determine the extent or significance of population changes in BC during the past century. In most cases this is due to insufficient data, rather than evidence for lack of change. All the anecdotal evidence, and most of the quantitative data indicate declines in populations rather than stable or increasing populations. At-sea surveys from 1979-1982 in Barkley and Clayoquot Sound (Carter 1984, Sealy and Carter 1984) provide the only replicated sampling from more than a decade back that can be compared with more recent counts (Kelson et al. 1995, Kelson and Mather 1999, Burger 2000). These all indicate declines in populations, but as discussed above, the causes and extent of the declines are not clear. Additional data from future years should allow long-term trends to be separated from the confounding effects of inter-annual variability and ocean conditions, such as sea temperature. Radar counts of murrelets entering watersheds seem to have less short-term variability than at-sea counts and are therefore more likely to detect long-term trends.

Comparison of habitat capability (potentially useful nesting habitat) and habitat suitability (currently available habitat) provides some indication of the loss of habitat that has occurred through coastal BC (see section 4.6.3).

3.4 Population size and trends in the United States

California – The population size is estimated at about 6000 birds (Ralph and Miller 1995), although estimates from 2000 suggest a smaller population (Table 3.5). Breeding success and recruitment appear to be low in California, based on a small sample of nests and low juvenile:adult ratios recorded at sea (U.S. Fish and Wildlife Service 1997).

Oregon – Early estimates based on at-sea surveys suggested a population of 15,000-20,000 birds (Strong et al. 1995), whereas aerial surveys indicated 6,400-6,800 birds (Varoujean and Williams 1995). More recent estimates indicate something in between (Table 3.5)

Washington – Data from 2000 indicate a population of 6400 birds (Table 3.5).

Data from the Northwest Forest Plan (2000) – Population estimates from at-sea surveys using DISTANCE method line transect methods have been summarised for the area covered by the Northwest Forest Plan (Table 3.5, from Bentivoglio et al. 2002). In total these data show a population of about 18,000 birds in the states south of BC.

Table 3.5. Population estimates from Washington, Oregon and California provided by the Northwest Forest Plan Marbled Murrelet Effectiveness Monitoring (Bentivoglio et al. 2002).

		• ,	
Zone	Area	Population estimate	95% confidence interval
1	Puget Sound, San Juan Islands and Strait of Juan de Fuca	5635	3198 - 8453
2	Outer Washington Coast	769	500 - 1100
3	Northern and Central Oregon	6738	3940 - 11,707
4	Southern Oregon and Northern California	4876	4135 - 8100
5	Central California	78	13 - 168
All zones		18,097	12,991 - 23,202

There are reports of major declines in all three of these states but few actual count data to assess past changes (Ralph et al. 1995a, U.S. Fish and Wildlife Service 1997). Old-growth forests have been reduced by 85-95% in California and by about 82% throughout western Oregon and Washington compared to pre-logging levels (U.S. Fish and Wildlife Service 1997). Varoujean and Williams (1995) suggested that the Oregon and Washington populations had remained stable over the decade before 1995, but this conclusion is considered unsubstantiated (U.S. Fish and Wildlife Service 1997).

Alaska – The bulk of the world population breeds in Alaska, with most found in south-central and south-east Alaska. The most recent estimate indicates a population of 655,000-1,062,000 birds, based on randomly-distributed at-sea transects (Agler et al. 1998), but estimates using a variety of at-sea census data suggested a population in the low 100,000s, possibly 280,000 birds (Piatt and Naslund 1995). The differences in these population estimates reflects the difficulty of censusing the species over its vast and complex marine range in Alaska. This population appears to be declining (Piatt and Naslund 1995, Piatt 1998), although the declines evident in Christmas Bird Counts have been disputed (Hayward and Iverson 1998). The well-studied population in Prince William Sound has declined significantly since 1972 due to the combined effects of the *Exxon Valdez* oil spill, and the changes in the marine ecosystems (Kuletz 1996, Kuletz et al. 1997, Irons et al. 2000; see sections 5.4 and 5.5).

3.5 Metapopulations

There is not much evidence to determine the degree of isolation and movements among spatially isolated sub-populations (metapopulations) of Marbled Murrelets. The sparse information available suggests that behavioural interactions and perhaps gene flow occur readily among birds from local sub-populations. Breeding adults are highly mobile at sea, and birds from many breeding areas mingle at productive foraging sites during the breeding season (Whitworth et al. 2000, Hull et al. 2001a, Bradley 2002). Radar surveys in Clayoquot Sound (Burger 2001, 2002) and on the Olympic Peninsula (Raphael et al. 2002) suggest some movement of birds among watersheds from year to year. Radio-telemetry has shown that many birds routinely forage in the same general areas (Bradley 2002), but a few birds have been tracked making substantial changes in foraging sites, including crossing overland from the west to the east of Vancouver Island (F. Cooke, pers. comm.). Moulting and wintering aggregations probably include murrelets from widespread sub-populations, although some birds appear to remain near breeding areas (Rodway et al. 1992, Burger 1995a, Beauchamp et al. 1999). Genetic variation across the range is low (see section 2.1), but there are indications of morphological variations among sub-populations in BC. Significant differences in culmen (beak), wing chord and tarsus (leg) dimensions were found between birds from Mussel Inlet and Desolation Sound, suggesting some differentiation between these populations (Hull et al. 2001b).

There are no data on the size of isolated metapopulation that is required for long-term persistence, or on the likelihood of re-establishing populations in small habitat patches that "wink-out" (are temporarily extirpated). These appear to be fruitful fields for simulation modelling using information on the demographics, movements, fidelity, habitat requirements, and population size relative to habitat area. An understanding of the behavioural processes involved in pair formation, selection of nesting habitat, and inland spacing behaviour is needed to accurately model metapopulation dynamics.

4 INLAND HABITAT

4.1 Interpreting habitat associations: some cautionary notes

Interpreting habitat associations or preferences in a declining population is difficult. We cannot assume that the remnants of once widespread and common species have settled on the most favoured habitat (Caughley 1994). The remnant populations are most likely to end up in the habitat least favourable to the agent of decline, which through much of the murrelet's range appears to be the logging industry. Such constraints affect many of the studies reviewed below, especially those from southern BC through California. These studies are valuable in assessing current habitat use, and are essential for planning conservation and recovery strategies in these areas, but habitat associations important in areas with severely modified habitat might have limited application elsewhere. The converse is sometimes also true – habitat associations derived from relatively pristine areas might have little relevance for conservation management where the optimal habitats are no longer readily available. In the BC context this is important because the most detailed habitat analyses have been done on the Sunshine Coast (Desolation Sound and nearby areas) where the habitat is greatly modified or on the southwest coast of Vancouver Island (Clayoquot Sound and Carmanah-Walbran) where there has been much less habitat loss.

Several methods have been used to assess habitat use in Marbled Murrelets and all have advantages and limitations. Audio-visual surveys which record detections of murrelets seen and heard in dawn surveys were among of the first methods to be used inland. They have been used in numerous studies to determine the presence and occupancy of Marbled Murrelets in forest stands, and to assess habitat use (reviewed below). Over more than a decade the methods have been refined and standardized across the Pacific Northwest (Evans et al. 2000) and in BC (RIC 2001), and this remains the most widespread method for assessing the presence and relative abundance of murrelets in various habitats. The greatest limitations of audio-visual surveys are that:

- detections do not give reliable and accurate indicators of the actual numbers of murrelets present in a particular stand (Rodway et al. 1993a, Paton 1995);
- detections show high diurnal and seasonal variability and are strongly affected by weather, especially cloud cover and rain (Rodway et al. 1993a, Naslund and O'Donnell 1995, Jodice and Collopy 2000, Rodway and Regehr 2002);
- they do not show the actual sites used for nesting, although they are useful in locating nests;
- visibility (canopy opening) and to a lesser extent noise (streams etc.) can affect detections (Rodway and Regehr 2000, 2002);
- differences among observers adds variability to the data, despite efforts to standardize training and observation techniques;
- ground-based observers cannot access all the forests accessible to murrelets.

These limitations can be minimized through having large samples, selecting sampling stations with comparable visibility, statistically controlling the variability due to seasonal, annual, visibility and weather-related effects, focusing analysis on the sub-set of detections indicating

stand occupancy and subcanopy activity, and omitting detections of birds not seen or obviously commuting elsewhere. Examples including most of these treatments are in Bahn (1998) and Rodway and Regehr (2002). Detection data are more reliable as indicators of habitat suitability if combined with independent measures of habitat suitability, such as the availability of nest platforms and epiphyte cover (Chatwin et al. 2000, Rodway and Regehr 2002). Audio-visual surveys also provide information on the presence and relative abundance of potential predators (Burger et al. 2000a, Rodway and Regehr 2002), although they do not substitute for detailed censusing of predators.

Most Marbled Murrelet nests have been found using ground searches or selective tree climbing. In the first method audio-visual observations reveal murrelets landing on trees or narrow the search to likely tree patches. In the second method likely looking trees are climbed to search for nests. Both these methods are likely to lead to biased samples of nest sites and nesting habitat because observers do not randomize their searches or observation stations across all habitat types. Huettmann et al. (in prep.) have shown that nest sites accessible to people might have different habitat attributes than those on steep cliffs and other sites difficult to access. These biases can be reduced using a stratified random selection process covering all habitat categories to select trees for climbing. There are two additional benefits to this approach:

- the climber can record valuable information on canopy microstructure (platform size, epiphyte cover), tree height, presence of arboreal mammals and other important variables from a large sample of trees in all habitat categories;
- if sufficient trees are climbed the study will give estimates of nests density (nests per tree and nests per ha) which are not possible from any other method.

Attempts to use randomized climbing have shown that large samples of trees are needed to find sufficient nests to estimate densities (Rodway and Regehr 1999, Conroy et al. 2002), but the costs and benefits of this method relative to radio-telemetry have not been fully investigated.

Radio-telemetry eliminates most of the bias in locating nests and sampling nest habitat. The birds are caught on the water and tracked by aircraft and on foot to nest sites. The method has been successfully developed in Desolation Sound (Lougheed et al. 1998, Cooke 1999, Hull 2000), and is being used in Mussel Inlet, Clayoquot Sound and Queen Charlotte Islands/Haida Gwaii in BC (Kaiser and Keddie 1999, Hull 2000, Manley et al. 2001), and in several studies in the U.S. In addition to locating nests and hence nesting habitat, this approach yields a wide range of additional opportunities to study murrelets (Lougheed et al. 1998, 2002a,b, Vanderkist et al. 1999, 2000, Cooke 1999, Hull 2000, Bradley 2002, Bradley et al. 2002, Hull et al. 2001a, 2001b, 2002). These include:

- banding and recapturing birds for capture-mark-recapture estimates of survival;
- measuring of the chronology of breeding:
- estimating of the age structure and proportions of birds breeding
- providing blood and other tissue samples for genetic and physiological studies;
- providing morphometric data;
- determining the roles of males and females in incubation and chick-rearing;
- opportunities to study diving behaviour, movements, distribution and moulting locations of tagged individuals;
- measuring commuting distances between foraging areas and nest sites;

• establishing the links between marine and inland habitat use of individuals, and thereby allowing coordinated strategies for both marine and inland habitats.

The disadvantage of this approach is primarily the high cost of the entire venture, which limits its widespread application. Extrapolation of habitat and demographic data from a few intensively studied areas to the whole province seems risky, unless there are independent tests in other parts of the province. Radio-signals can be attenuated by vegetation, and there have been few tests to determine whether radio-signals from dense valley-bottom canopies are as detectable from a helicopter as those from sparse upper slope patches.

The telemetry data can be used to verify and test results from other methods. For example, on the Sunshine Coast the nest trees found by telemetry (R. Bradley, unpubl. data) were almost identical in size to those found by ground searches and tree-climbing (Manley 1999), confirming that the latter sample was not necessarily biased (see Table 4.2). Multivariate analysis of the habitat used for 45 nests found by telemetry in Desolation Sound (Waterhouse et al. 2002) provided similar results to the habitat suitability model developed in Clayoquot Sound from audio-visual and vegetation sampling data by Bahn and Newsom (2002a).

4.2 Habitat at nest sites

This section considers the characteristics of nest sites at the smallest (microhabitat) and element (nest tree) spatial scales.

About 200 nests of Marbled Murrelets have now been described, and more than half of these were in BC (Nelson 1997, Manley 1999, Hooper 2001, R. Bradley and F. Cooke, unpubl. data). By far the greatest number in BC has been reported from the Sunshine Coast, as a result of intensive research there (Manley 1999, R. Bradley and F. Cooke, unpubl. data). Most of the Sunshine Coast nests were found in areas subjected to intensive logging where little of the low elevation and big-tree old-growth remain (Manley and Jones 2000, Demarchi and Button 2001a,b). Relatively few nests have been reported from Vancouver Island and Queen Charlotte Islands/Haida Gwaii, which support a large proportion of the breeding population, and none from the northern mainland where the population size remains largely unknown. Because the BC sample is so heavily biased by the large Sunshine Coast sample, interpretation of averages and even ranges of habitat parameters based on pooled data is difficult and might not be relevant to other areas with differing topography, biogeoclimatic zones and logging histories. This section focuses on nest habitat parameters which are relevant to conservation and management. Reviews of other measures, such as the dimensions of nest cups and their location on branches, can be found in Nelson (1997) and Hooper (2001).

4.2.1 Tree nests

Tree species - All tree nests in North America have been in conifers, with the exception of a single nest found in a red alder (*Alnus rubra*) in BC (details below). In BC most nests have been found in yellow cedar (*Chamaecyparis nootkatensis*), western hemlock (*Tsuga heterophylla*),

Sitka spruce (*Picea sitchensis*), Douglas-fir (*Pseudotsuga menziesii*), and western red-cedar (*Thuja plicata*), with fewer in mountain hemlock (*Tsuga mertensiana*) and amabilis fir (*Abies amabilis*)(Table 4.1). The nest in a red alder, the first found in a deciduous tree, was one (3%) in a sample of 30 nests found by radio-telemetry in Desolation Sound and Mussel Inlet (Bradley and Cooke 2001). Elsewhere, a few red alders and broad-leafed maple (*Acer macrophyllum*) have been climbed and found to offer few potential nest sites (Rodway and Regehr 1999).

Most researchers concur that murrelets do not appear to select specific tree species but are more likely to use those species that locally provide suitable platforms, i.e., Sitka spruce or western hemlock in low elevation forests of SW Vancouver Island, or yellow cedar in the higher forest patches of the Sunshine Coast. For this reason, and because of the unequal sampling across the province, range-wide or provincial totals cannot be used as a guide to the most suitable trees in a local area.

Table 4.1. Tree species in which nests of Marbled Murrelets have been found.

Tuble 4.1. Tree spe		British C				
	SW	SE		Queen	='	
	Vancouver	Vancouver	Sunshine	Charlotte		CA, OR
Tree species	Island	Island	Coast	Islands	Alaska	& WA
Western hemlock	6	0	13	0	6	15
Mountain hemlock	1	0	2	0	9	0
Douglas-fir	0	3	11	0	0	39
Sitka spruce	11	0	0	0	5	1
Western red-cedar	2	0	9	1	0	1
Yellow cedar	1	0	60	0	0	0
Amabilis fir	1	0	1	0	0	0
Coast redwood	-	-	-	-	-	9
Red alder	0	0	1	0	0	0
Total	22	3	97	11	20	65
	Hooper					
	2001,					
	Burger,		Hooper			
	unpubl.,		2001,			
	Bradley &		Bradley &	Dechesne		
	Cooke	Burger et	Cooke	& Smith	Nelson	Nelson
Source	unpubl.	al. 2000	unpubl.	1997	1997	1997

Tree size and nest height – Data on the height and diameter at breast height (DBH) of nest trees, and the height of nest limbs show clear regional differences (Table 4.2). Nests from outside BC are included for comparison. Nests from Vancouver Island, Oregon and Washington were in larger trees than those from the Sunshine Coast, Queen Charlotte Islands/Haida Gwaii and Alaska. There are several explanations for this. First, tree size is affected by latitude and climate, which partly explains the use of smaller trees in Alaska and Queen Charlotte Islands/Haida Gwaii. Second, low-elevation logging has removed most of the larger trees in the Sunshine Coast, but large trees remain on parts of Vancouver Island, Oregon and Washington. Third, many of the nests found on Vancouver Island were from searches focused on low elevation areas with very large trees. Conroy et al. (2002) did search for nests in higher elevations in Clayoquot Sound

but found none. By contrast, nest searches on the Sunshine Coast covered a wider range of elevation and habitat types, and many came from tracking radio-tagged birds without any elevation or habitat restrictions.

Table 4.2. Summary of nest height, and height and diameter at breast height (DBH) of nest trees.

	No. of Nest height (m)		Tree height	Tree height (m)		m)	_	
	nests	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Source
SW Vancouver Island								
Carmanah-Walbran		41 ± 8	31-54	69 ± 8	56-80	239 ± 66	133-370	Burger, unpubl.
Clayoquot Sound (random climbing) Clayoquot Sound	5	31 ± 9	19-40	42 ± 4	38-48	171 ± 92	60-310	Conroy et al. 2002
(telemetry)		-	-	36 ± 12	26-58	90 ± 23	55-119	R. Bradley, unpubl.
SE Vancouver Island	3	33 ± 5	29-40	47 ± 12	40-61	134 ± 26	119-165	Burger et al. 2000
Sunshine Coast								
Caren range	1	17.4	-	30	-	93	-	Jones 1993
Bunster range	52	20 ± 1	12-30	28 ± 1	17-45	100 ± 3	60-153	Manley 1999
Telemetry sample	17	33 ± 9	18-45	47 ± 11	30-69	123 ± 54	36-250	R. Bradley, unpubl.
Queen Charlotte Is.	1	11	-	15	-	-	-	Dechesne & Smith 1997
Alaska	20	15 ± 4	9-24	24 ± 5	15-34	66 ± 23	27-120	Nelson 1997
Washington	6	34 ± 13	20-53	57 ± 8	45-65	150 ± 45	89-220	Nelson 1997
Oregon	31	28 ± 2 (SE)	10-75	51 ± 2 (SE)	34-85	117 ± 7 (SE)	49-213	Nelson & Wilson 1999

Tree age – With the exception of the single alder mentioned above, all of the trees containing nests in BC would be classified as old-growth conifers, based on their size, structure, epiphyte loads and, in many cases, evidence of senescence. All were likely >140 years old, and most >200 years old. In Oregon five nests have been found in mature (95-250 year old) and young (66 year old) western hemlock trees, which had large branches formed by mistletoe (Nelson 1997). There has been no evidence that mistletoe deformities provide nest platforms in BC.

Nest location within trees – Nests are typically on large boughs; in BC limb diameters at the trunk ranged from 15 to 74 cm, and across the species' range from 7 to 74 cm (Nelson 1997, Hooper 2001). In most locations the nest limbs support thick mats of moss and other epiphytes, and the nests are merely depressions in the epiphyte mat. In drier areas, such as Douglas-fir forests, layers of accumulated duff and litter form the nest substrate. It is not clear to what extent the availability of moss or other soft substrates might limit nesting. While the great majority of nests have been found on mossy mats or soft litter substrates, two nests in California were on limbs with no soft substrate and were laid on bare bark (Nelson 1997). In cool, windy climates the insulation provided by moss might be important. Two nests have been found in the remains of old bird (likely pigeon) or squirrel nests (Nelson 1997).

Nests might be placed on any suitable platform along the bough. Nests have been found up to 7.6 m from the trunk, but most are at or near the base of the limb near the trunk (Nelson 1997). Most nests are in sites sheltered under overhanging foliage (Nelson 1997, Manley 1999). This cover evidently provides some protection from weather, and reduces the risk of detection by predators.

The most detailed examination of microsite selectivity was done by Manley (1999). Limbs with nests were significantly larger in diameter, had a larger flat platform surface, and were more likely to have overhead foliage cover than limbs in the same trees with no nests. Epiphyte cover influenced nest site selectivity. Most nests were on limbs with thick moss; limbs with bare platforms and those with thin moss or lichen/litter layers were avoided.

Nest trees compared with other nearby trees – Nests are typically in the largest trees in the stand (Nelson 1997). Two studies in BC and one in Oregon compared the size and structure of trees with nests with randomly selected trees with platforms in the same forest stand or other stands. Comparison between nest trees and those with platforms nearby is a stronger test for likely nest characteristics than if nest trees were compared with all randomly selected trees, many of which would not provide potential nest platforms.

On the Sunshine Coast, Manley (1999) compared 52 trees with nests with 204 other trees with potential nest platforms (limbs or other structures >15 cm in diameter) in the same stands. Nest trees were significantly larger in diameter, had a larger number of potential nesting platforms, and were slightly but significantly taller (Table 4.3). Nest trees were associated with significantly larger gaps in the canopy than the other trees. There was no difference in the availability of mossy platforms. Murrelets showed significant selectivity for tree species. Yellow cedars, which contained most nests and most frequently provided potential nest platforms in this area, were used disproportionately more than their availability. Western hemlock and Douglas-fir were used for nesting, but less frequently than expected, and no nests were found in western red-cedar and amabilis fir trees.

Table 4.3. Characteristics of 52 nest trees compared with 204 other trees with platforms in the same plots on the Sunshine Coast (Manley 1999). Means ± SE shown.

Measure	Nest trees	Other trees	P-value
Tree diameter (cm)	100 ± 3	83 ± 2	<0.001
Tree height (m)	28.2 ± 0.8	26.0 ± 0.4	0.02
Potential platforms per tree*			
DBH range 61-90 cm	7.5 ± 0.8	2.8 ± 0.3	< 0.001
DBH range 91-120 cm	8.9 ± 1.1	4.5 ± 0.6	< 0.001
DBH range >120 cm	16.0 ± 5.0	4.9 ± 1.0	<0.01

*statistical tests on platform number per tree were applied only to yellow cedar, the most common nest tree species

From a range of habitats in Clayoquot Sound, Conroy et al. (2002) compared five trees with nests with 456 other randomly selected trees. Nest trees had significantly larger diameters (mean 171 ± 92 [SD] cm) than other trees (99 ± 46 cm), but there were no significant differences in height, number of potential nest platforms, or cover or thickness of epiphytes. This comparison was obviously limited by the small sample of nest trees.

Based on a four year study involving tree climbing in randomly selected stands in Oregon, Nelson and Wilson (1999) compared 21 nest trees with 284 trees with platforms in the same plot as the nest trees, and 640 trees with platforms in other plots within the same stands as the nest trees (Table 4.4). Compared to other trees in the same plot, the nest trees were significantly

larger, had more platforms and more of the larger platforms, more horizontal cover, and slightly but significantly deeper moss cover, but did not differ in the percentage of moss cover or the index of vertical cover. They did not test differences in tree height. Compared to trees in other plots but in the same stand, the nest trees had significantly more platforms, more larger platforms, more moss on the platforms, and more vertical and horizontal cover, but diameter, and moss on the trees did not differ significantly.

Table 4.4. Characteristics of nest trees compared with other trees with platforms in the nest plot and in other plots within the same stand in Oregon (Nelson & Wilson 1999). Means ± SE shown. Different letters in each row indicate significant differences, the same letter indicates no difference.

Characteristic	Nest trees	Platform trees in nest plot	Platform trees in other plots	ANOVA P-value
Tree diameter (cm)	116 ± 10 a	94 ± 2 b	102 ± 1 ab	<0.001
Platforms per tree	31 ± 5 a	17 ± 1 b	20 ± 1 b	<0.001
Large (= 15 cm) platforms per tree	24 ± 6 a	7 ± 1 b	8 ± 1 b	<0.001
% moss on tree	71 ± 5 ab	73 ± 1 a	69 ± 1 b	0.042
% moss on platforms	84 ± 2 a	80 ± 1 ab	79 ± 1 b	0.018
Moss depth on platforms (index)	2.8 ± 0.09 a	$2.5 \pm 0.03 b$	$2.4 \pm 0.03 b$	<0.001
Horizontal cover (index)	1.8 ± 0.06 a	$1.6 \pm 0.03 b$	1.6 ± 0.02 b	0.047
Vertical cover (index)	2.1 ± 0.07 a	2.1 ± 0.03 a	1.8 ± 0.02 b	<0.001

Summary of nest tree characteristics - It seems that given a choice, murrelets will select nest sites on boughs with the following five characteristics:

- sufficient height to allow stall-landings and jump-off departures;
- openings in the canopy for unobstructed flight access;
- sufficient diameter to provide a nest site and landing platform;
- some soft substrate to support a nest cup;
- and, overhead foliage cover.

The first four conditions are almost always found in old-growth trees which explains why the overwhelming majority of nests are in such trees, although the birds are obviously adaptable and might nest in sub-optimal sites which do not meet all these conditions. The proximal cues used by the birds to select nest sites are not known, but seem likely to be a combination of these five features. Murrelets, evidently prospecting birds, frequently land in trees in which no nests are found, indicating that several sites are considered before deciding on a nest site. One consistent pattern is that murrelets tend to nest in trees with many suitable platforms even though only one is needed for a nest site. They might be attracted to trees offering several possible nest sites.

4.2.2 Ground and cliff nests

In Alaska, nests have been found on the ground in a variety of locations, including mossy cliff ledges, among tree roots on cliffs or steep slopes, in rock crevices, under crevices and in the open (DeGange 1996, Nelson 1997). Most ground nests have been found on islands, or on mainland areas within 1 km of the ocean (maximum 6 km) with no large trees nearby (Nelson 1997, Marks

and Kuletz 2001), but four were found in forested areas near the ocean in south-central and south-eastern Alaska (DeGange 1996). DeGange (1996) reviewed ground nests in Alaska and found few common features: nests were on treeless islands, recently deglaciated terrain, among scrubby trees and on forest edges. Elevation of 12 nests ranged from 7 to 710 m. Four of nine ground nests were at the top of cliffs. Most nests had some cover from overhanging rock or vegetation directly overhead.

On the basis of at-sea distribution, Piatt and Ford (1993) estimated that 3% of the Alaska population nested in unforested places where they were likely to use ground nests. The more recent discovery of ground nests in forested areas in Alaska indicates that this proportion might be slightly higher in that state.

In British Columbia, Bradley and Cooke (2001) report one confirmed and two probable nest sites on cliffs used by radio-tagged birds on the central mainland (Desolation Sound and Mussel Inlet). All three were on steep slopes (70-90°) offering open flyways, at relatively high elevations (800-1300 m), within 15-21 km of the ocean, and were confirmed or suspected of being on mosscovered platforms surrounded by shrubby vegetation. At all three sites the mossy ledges and crevices provided many more potential nest platforms than available in adjacent trees (the nearest trees with platforms were >300 m, and >500 m away, respectively, at two of the sites). The high elevation and position on cliffs suggested that risk of ground predators was low. Kaiser and Keddie (1999) noted that the murrelet tracked to the cliff nest in Mussel Inlet had a deformed foot, which might have made it difficult to land on a narrow branch. Bradley and Cooke (2001) suggested that ground/cliff nests were relatively rare in their study area, and comprised 3% (1/30) of confirmed nests, and 3% (2/78) of suspected nest sites. Additional ground nests were found in Desolation Sound and on Vancouver Island in 2001, but details are not yet available. Rodway et al. (1991, 1993b) searched alpine areas in Queen Charlotte Islands/Haida Gwaii but found no evidence of nests or near-nest activity. No ground or cliff nests have been found south of BC (Nelson 1997).

It is not known whether individual birds might switch from tree to ground nests with the disappearance of suitable tree-nesting habitat. There are no significant genetic differences between birds from ground-nesting and tree-nesting populations in Alaska (Pitocchelli et al. 1995, Congdon et al. 2000). If there is strong habitat imprinting of nestlings, then the transition from one habitat to another might not be readily made. Chicks raised in tree or ground nests might be more likely to return to breed in their natal habitat.

4.2.3 Estimates of nest density

Estimates of nest density (nests per ha) have been made in several studies in BC by combining measures of nests per trees with platforms (from tree climbing) and density of trees with platforms per ha (from vegetation plots). In fragmented and heavily logged habitat on the Sunshine Coast, Manley (1999) estimated the nest density as 0.3-0.7 nests per ha, which apparently included nests active in previous years. Rodway and Regehr (1999) reported no nests in 70 randomly selected trees in valley-bottom habitat in the Ursus Valley, Clayoquot Sound, but estimated from a probability model that the maximum nest density in this habitat was likely to be

0.86 nests per ha. Conroy et al. (2002) increased the sampling effort in the Ursus and found 5 nests in valley-bottom habitat rated excellent. Combined with Rodway and Regehr's (1999) data, the estimate of nest density for this habitat was 0.66 ± 0.29 (SD) visible nests per ha. Considering only nests active in the year they were found, the density was 0.11 ± 0.12 (95% CI = 0 to 0.35) nests per ha (Conroy et al. 2002). No nests were found in a smaller sample of randomly-selected higher elevation trees in habitat ranked good or sub-optimal in the Ursus (Conroy et al. 2002). Using the same method of climbing randomly-selected trees, Burger and Bahn (unpublished data) estimated densities of 0.60 ± 0.35 (SD) nests per ha in valley-bottom habitat in Carmanah and Walbran valleys. Nests were visible for about 4 years after use and therefore this translates into 0.15 ± 0.09 active nests per ha per year. These data are insufficient to test whether nest density in more pristine habitat (e.g. Ursus Valley and Carmanah-Walbran) differs significantly from those in heavily logged and fragmented habitat (e.g., Sunshine Coast).

4.3 Stand-level habitat associations

This section evaluates the relationships among Marbled Murrelet nesting behaviour, nest-habitat requirements and stand-level habitat measures. There is naturally some overlap in the spatial scale and range of topics discussed here and those considered in sections on nest microhabitat (section 4.2) and landscape-level habitat associations (section 4.5).

This section has four parts, separated by the research strategy and type of data used to determine stand-level habitat associations. These include studies which:

- compared stands in which murrelets were known to nest with other stands in the same landscape units;
- related behaviour and audio-visual detections with habitat data in order to determine habitat suitability;
- compared the availability of microhabitat features known to be important to nesting murrelets (e.g., availability of platform limbs and epiphyte cover) with stand-level habitat measures;
- derived algorithms (combinations of habitat measures) which captured the important features in the habitat and allowed mapping of suitable habitat.

4.3.1 Comparing nest stands with other stands

On the Sunshine Coast, Manley (1999) compared the characteristics of 34 forest patches containing nests (plots of radius 25 m around nest tree) with randomly selected paired patches of the same size 60-200 m from the nest tree (Table 4.5). Nest patches had significantly fewer trees in total, fewer small trees (11-40 cm DBH), but more large trees (>60 cm DBH). There were no significant differences in snag densities. Nest patches had significantly higher densities of trees with platforms and the overall platform density in nest patch was almost three times higher than in random patches. These differences in tree density, tree size and platform density persisted even when the nest tree and its platforms were excluded from the comparison. Nest patches had significantly fewer platform limbs with little or no epiphyte cover than random patches, but there

was no difference in the proportions of limbs with high epiphyte cover. Nest patches had larger canopy gaps than random plots but this was not significant, and the size distribution of gaps was also similar. Finally, no significant differences were found between nest and random plots in slope, aspect, or vegetation site associations. In summary, the availability of large trees with high numbers of platform limbs was the major difference between nest patches and randomly-selected patches (some of which might also have been suitable for nesting).

Table 4.5. Summary of the main differences between forest patches with nests and randomly selected patches (34 pairs of patches) on the Sunshine Coast (Manley 1999). Means are given ± SE. See Manley (1999) for details of statistical tests.

Measure	Nest plots	Random plots	Р
Density of trees per ha by DBH size class			
DBH 11-40 cm	521 ± 31	695 ± 46	<0.01
DBH 41-60 cm	96 ± 61	102 ± 7	>0.10
DBH 61-90 cm	53 ± 5	38 ± 4	< 0.01
DBH >50 cm	107 ± 8	88 ± 7	< 0.05
DBH >90 cm	15 ± 2	9 ± 2	< 0.01
All live trees	685 ± 34	850 ± 44	<0.01
Density of trees with platforms per ha	32 ± 4	18 ± 3	<0.01
Density of platforms/ha	129 ± 14	47 ± 9	< 0.001

Waterhouse et al. (2002) made a stand-level analysis of the habitat used for 45 murrelet nests, all in trees, located by radio-telemetry in the Desolation Sound area, Sunshine Coast. A complementary landscape-level analysis of these telemetry nests by Huettmann et al. (in prep.) is summarised in section 4.5.1. Habitat features were extracted from aerial photographs, and coded in the same way as in the Vegetation Resources Inventory (VRI) databases (RIC 1997) commonly used for management purposes in BC.

Waterhouse et al. (2002) performed a series of comparisons, using all nests (n = 45) and a sub-set of nests which reached the mid-chick stage (n = 22). Habitat in forest polygons containing nests was first compared with habitat in randomly selected polygons adjacent to the nest polygons. This pairwise comparison helped control for possible effects of elevation and distance from the sea. Next, nest polygons were compared with randomly-selected adjacent polygons that were treed (>10% crown cover) but did not necessarily contain potential nest platforms, and a final comparison was then made with random adjacent polygons which contained potential nest platforms.

All nest polygons were treed, but 9% were not fully treed. Among the random adjacent polygons, 44% were not fully treed and an additional 18% were treed with younger seral stages (<140 years). This indicates that the murrelets were often nesting in treed areas, bordered by young forest, clearcuts or other non-forest habitat, and nests were not necessarily located towards the interior of large continuous stands of old-growth.

Compared with randomly-selected treed polygons, the nest polygons were significantly older, and had taller trees, larger mean basal area, and greater vertical complexity (Table 4.6). There were

no significant differences in crown closure. There were fewer differences between nest polygons and those random polygons that contained potential nest platforms; the nest polygons were significantly older and had greater vertical complexity, but did not differ in other attributes (Table 4.6).

Table 4.6. Results from comparisons of polygons with nests with randomly-selected adjacent polygons that were treed (had >10% tree cover), and were treed with potential nest platforms (Waterhouse et al. 2002). Two sets of comparisons were made: the first included all nests for which there were habitat data, the second only nests which were known to reach the mid-chick stage.

Means (± SE) are shown for all attributes, except for vertical complexity, where the number of polygons classified as 1 (very uniform - uniform) and 2 (moderately uniform to non-uniform) is shown

for each polygon type.

	All nest polygons (n = 45)				Mid-chick nest polygons (n = 22)			
Attribute	Nest polygon	Random treed polygon	Random polygons with platforms		Nest polygon	Random treed polygon	Random polygons with platforms	
Crown closure (%)	48 ± 3	52 ± 3	50 ± 3		47 ± 3	52 ± 4*	50 ± 4	
Age classification (years)	255 ± 11	166 ± 18***	215 ± 16*		282 ± 11	144 ± 27***	214 ± 25*	
Mean tree height (m)	30 ± 1	21 ± 2***	26 ± 2		30 ± 2	18 ± 3***	25 ± 3	
Mean basal area (sq.m)	56 ± 4	39 ± 4*	49 ± 4		55 ± 5	34 ± 7*	48 ± 7	
Vertical complexity 1	9	27***	19*		4	16***	10	
Vertical complexity 2	33	15	20		15	3	8	

^{*}P<0.05; **P<0.01; ***P<0.001 (Compared with nest polygons - see Waterhouse et al. 2002 for details)

If only polygons in which breeding attempts reached mid-chick stage were considered, then nest polygons had significantly lower crown closure (but only a 5% difference), and significantly older age, taller trees, larger mean basal area, and greater vertical complexity than random treed polygons (Table 4.6). Mid-chick nest polygons were significantly older than random polygons with platforms, but no other attributes differed significantly.

Logistic stepwise regression models in this analysis suggested that vertical complexity of the canopy was an important predictor of the conditional probability of a murrelet using a polygon, and of reaching the mid-chick stage. The effects of canopy complexity persisted for the full range of forest age-classes and tree heights considered in the models. Nest polygons tended to be less uniform with more canopy gaps, had more patchy stocking and had greater height differences (>21%) between the leading tree species and the average tree layer.

Models considering age and vertical complexity as covariates showed that polygon suitability continued to improve as forest age increased beyond 140 years of age (the minimum age considered to provide suitable murrelet habitat in BC). The rate of improvement tended to level off beyond 200 years of age. Age was considered to be a surrogate for microhabitat features such as platform size and epiphyte cover. Polygons with nests that reached mid-chick stage were a minimum of 150 years old.

Models including tree height and vertical complexity as covariates indicated that murrelets were more likely to nest in polygons that had taller trees and were more vertically complex. Conversely, polygons with shorter trees might be more likely to be used for nesting if they had vertically complex canopies.

There was broad congruence in the habitat models produced by Bahn and Newsom (2002a; see section 4.6.2 for details) in Clayoquot Sound and Waterhouse et al. (2002) in Desolation Sound. The former study used audio-visual surveys, vegetation plots and mapped variables derived from Vegetation Resources Inventory (VRI) data (RIC 1997). The latter study compared polygons with nests, located by radio-telemetry, with randomly-selected adjacent polygons with trees, and used interpretation of aerial photographs to provide habitat measures similar to those in VRI databases. Both studies concluded that the combined effects of vertical complexity, tree height, and forest age were significant predictors of nest habitat suitability. Murrelets were more likely to nest in forests which had complex canopies, with older, taller trees. Crown closure and basal area were useful predictors in Bahn and Newsom's (2002a) model but were not selected in those of Waterhouse et al. (2002). Bahn and Newsom also included elevation and distance to sea in their model but these were not considered in the models of Waterhouse et al. (2002).

In the Ursus Valley, Clayoquot Sound, Conroy et al. (2002 and unpubl. data) compared five plots containing a nest (radius 15 m centred on nest trees) with 39 randomly-selected plots of the same size. Compared with the random plots, nest plots had significantly more epiphyte cover on branches and taller trees with larger diameters, but there were no differences in tree densities or in densities of platforms per ha (Table 4.7). This comparison is somewhat limited by the small sample of nest plots, and the fact that all the nests were found in habitat rated "excellent", whereas the other random plots were distributed in "excellent" (50% of plots), "good" (31%), and "sub-optimal" (19%) habitat categories.

Table 4.7. Comparison of habitat measures between 5 forest plots with nests and 39 randomly selected plots in the Ursus Valley, Clayoquot Sound (C. Conroy unpubl. data). Means are given ± SE. One-way ANOVA was used to compare groups.

	Nest plots	Random plots	Р
Mean epiphyte cover score	3.1 ± 0.6	1.5 ± 0.2	0.012
Mean tree height (m)	26 ± 3	18 ± 1	0.033
Mean DBH (cm)	52 ± 6	39 ± 2	0.033
Density of trees with platforms per ha	48 ± 15	44 ± 5	0.81
Density of platforms/ha	156 ± 89	215 ± 32	0.53

In Oregon, Nelson and Wilson (1999) compared 30 plots centred on nest trees (25 m radius) with 123 similar plots at randomly selected sites within the same stand as each nest tree. Trees in nest plots had significantly more moss (on trees and on platforms), deeper moss, more mistletoe, larger platforms, more platform trees per plot, more canopy layers, and more vertical and horizontal cover than plots with no known nests (Table 4.8). Nest plots also had more western hemlock trees with platforms, and were closer to man-made edges than randomly selected plots. No significant differences were found in tree density, density of large trees (>80 cm DBH), mean

tree height, mean platform height, mean platform density per ha, canopy cover or distance to stream (data not shown here).

Table 4.8. Comparison of habitat measures showing significant differences between 30 plots with nests and 123 plots with no known nests in the same stands in Oregon (Nelson and Wilson 1999). Means ± SE are shown.

Measure	Nest plots	Other plots	P-values
% moss on tree	81 ± 4	64 ± 2	0.007
% moss on platforms	81 ± 3	74 ± 3	0.054
Moss depth (index)	2.5 ± 0.1	2.2 ± 0.1	0.037
% mistletoe on tree	24 ± 10	11 ± 2	0.024
Trees with platforms (25 m radius)	9.4 ± 1.3	4.9 ± 0.4	<0.001
No. platforms (25 m radius)	101 ± 12	57 ± 6	<0.001
Mean platform diameter (cm)	15.8 ± 0.4	13.8 ± 0.5	0.002
No. of canopy layers	2.5 ± 0.1	2.2 ± 0.04	0.024
Horizontal cover index	1.9 ± 0.09	1.6 ± 0.05	0.044
Vertical cover index	2.1 ± 0.08	1.8 ± 0.05	0.012
Slope (%)	38 ± 3	48 ± 2	0.026
Distance to man-made opening (m)	64 ± 8	93 ± 6	0.018

4.3.2 Audio-visual detections as indicators of suitable habitat

Many studies in the United States (Table 4.9) and British Columbia (Table 4.10) have compared measures of murrelet activity from audio-visual surveys with habitat parameters in the surrounding forest. In general there were two types of statistical comparisons:

- those that compared stations showing murrelet occupancy with some other subset of the sampled stations, such as a random selection (e.g., Grenier and Nelson 1995), or stations without occupancy or without evidence of murrelets (e.g., Kuletz et al. 1995a,b); and,
- those that compared the frequencies of detections, occupied detections or subcanopy detections with the habitat parameters, using either correlations, ANOVA, or some other procedure to reveal significant associations (e.g., Rodway and Regehr 2002).

The former approach is more common in Washington, Oregon and California, where evidence of occupancy usually provides some measure of protection of the stand. The second approach has been more commonly used in BC because occupancy does not automatically confer protection of stands, and identification of highly suitable habitat, rather than occupied habitat, is an important goal. Some studies combined both approaches.

In this review, positive associations were identified as habitat parameters that were associated with high frequencies of detections or with occupied stations. Negative associations were those showing no or little evidence of occupancy or activity. For studies that did not use statistical tests, and for statistical studies where trends approached significance or were limited by sample size, the trends were shown with + or - symbols in parentheses. See Tables 4.9 and 4.10 for symbol key. Presenting the data from many studies in this summarized form helps to assess the general trends in habitat associations, but most studies involved complex ecosystems and there

were often environmental or study-design factors which affected the habitat associations. A few explanations are therefore needed for each study, and some habitat associations not summarized in the tables require comment.

In Alaska, the two studies by Kuletz et al. (1995a,b) involved relatively large populations of murrelets, and all available forests were often close to the ocean (<10 km). In south-central Alaska, a multiple regression model which explained 52% of the occurrence of occupied behaviour selected proximity to the head of bays, elevation, slope, aspect, % forest cover, tree diameter and epiphyte cover on branches as significant factors (Kuletz et al. 1995a). On Naked Island forest types were classified using timber volume and tree size and most murrelet detections and all 10 nests were found in the two categories with largest trees and highest volume (Kuletz et al. 1995b).

Studies in California, Oregon and Washington usually covered highly fragmented forests with relatively small stands of old-growth. Most emphasis here was placed on identifying the critical features of stands with occupancy. In Washington, differences in detection frequencies and percentage stand occupancy were found among physiognomic provinces, (equivalent to biogeoclimatic zones in BC) with high values found in provinces with moister ecosystems favouring large trees (Hamer 1995). This was also reflected in the positive association with mosses (abundant in moister forests) and negative association with lichens (in drier forests). Hamer found that the presence of platforms had a stronger positive association with murrelets than tree size (DBH), but the former measure was not available from vegetation maps and so tree size was the most useful mappable measure. Sitka spruce, followed by large Douglas-fir were the tree species providing the most suitable structure for murrelets, but western hemlock also showed a significant positive association. The positive association with slope (Table 4.9) found in Washington appears to be an artifact caused by the removal of most old-growth in the coastal lowlands for cities, agriculture, logging etc.

Grenier and Nelson's (1995) analysis from Oregon covered a large sample of stations (Table 4.9). Stem density was lower at occupied than at randomly selected stations, except for the density of larger trees (>66 cm DBH) when it was higher. Association was positive for timber volume of conifers but not for hardwoods. This reflects avoidance of second-growth and smaller trees.

Miller and Ralph (1995) analysed two types of forest in central and northern California. The first was in remnant stands of old-growth in areas heavily harvested (Table 4.9: stands), and the second in more contiguous, larger tracts of forest in protected areas (parks). Relatively few parameters were tested, but tree size (DBH and height) and the occurrence of platforms were identified as key habitat parameters for murrelets. In the park areas, detections were three times more common within the major drainages than on major ridges, and elevation had a negative influence. Murrelet detections dropped off beyond 40 km of the ocean. Coast redwoods and Douglas-fir showed positive associations with murrelets.

Table 40	Chand lavel habita		Manhiad Museula	ts in the United States
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Table 4.9. Stand-level habitat asso				Oneman (Chata In :!-)	Oregon (Cuielaux)	California (ataw -!-)
Location	Scentral Alaska		Western Washington		Oregon (Suislaw)	California (stands)
Reference	Kuletz et al. 1995a	Kuletz et al. 1995b	Hamer 1995		Grenier & Nelson 1995	Miller & Ralph 1995
Biogeoclimatic zone or equivalent		Hemlock/Spruce	Various	Mostly Douglas-fir	Mostly Douglas-fir	Redwood/Douglas-fir
No. of stations/sites	262	72	151	388	120	286
Years of study	3	1	3	1	3	2
MaMu measure	No. of detections &	No. of detections &		Occupied stands vs.	Occupied stands vs.	Detection frequency &
	Occupied vs. Other	Occupied vs. Other	Occupied stands	randomly selected	randomly selected	Occupied vs. Present
	stations	stations	vs.Unoccupied	stands	stands	vs. Undetected
Macro-habitat parameters						
Distance from ocean		AII <1.2 km	NS, -ve beyond 64km			NS
Elevation	-*/NS		_*		NS	
Slope	NS	NS	+*		_*	
Aspect	NS	NS	NS		NS	
Stand area		NS				NS
Total forest cover	+*	+*/NS				
Stem density			+*	*- or NS		
Density of large trees (>80						
cm dbh)				+* (>66 cm dbh)		+*
Tree age				+*	+*	
Canopy closure	+*	NS	_*		_*	
Basal area of trees				NS	NS	
Timber volume		+*		+* (conifers)		
Tree diameter (dbh)	+*	+*	+*	+*	+*	
Tree height	+*	NS	+*		+* or NS	
Density of snags					NS	
Tree characteristics						
Epiphyte cover on branches	+*	Moss +*	Moss +*, Lichens -*			
No. of potential platforms/tree	+*		+*			
No. of potential platforms/ha			+*			
Mistletoe score			+*			
Associations with tree species			•			
Sitka Spruce			NS (+)			
Western Hemlock			+*		NS	
Mountain Hemlock			NS (-)		NS	
Western Red-cedar			• • •		NS	
Yellow Cedar			NS (+)		N3	
			NC ()			
Amabilis Fir			NS (-)		ı * whon large	+*
Douglas-fir	_*		NS (+)		+* when large	+ "
Red Alder	-"					
Coast Redwood	1.11 1 41: -14:	I II ale a a a a 40 olfo o				+*
	Higher activity near	Higher activity near				
Other relevant results Key + : positive association with	heads of bays	heads of bays	1			

Key +: positive association with (+): +ve trend but no statistical test
-: negative association with (-): -ve trend but no statistical test
*: significant statistical test NS: not significant (statistical test)

Within BC the most detailed investigations of murrelet-habitat associations have been in the multi-year studies in Clayoquot Sound. The analysis by Rodway and Regehr (2002) covered 284 stations in 10 watersheds, four biogeoclimatic subzones (Coastal Western Hemlock CWHvh1, -vm1, -vm2 and Mountain Hemlock MHmm1), and a wide range of elevations and old-growth forest types. Many positive and negative associations with murrelet detection frequencies were identified (Table 4.10). Two sets of associations are presented here: the first set contains correlation coefficients from the raw data; the second set (controlled) shows the results after statistical controlling of factors found to affect detections (weather, date, year, visibility at the station). When tree species are considered, associations are shown separately in Table 4.10 for all trees and for large trees (>80 cm DBH). Overall, the three key factors appeared to be: density of trees with platforms; density of large trees; and mean DBH (Rodway and Regehr 2002).

Rodway and Regehr (2002) also considered possible effects from biogeoclimatic subzones and site series. Some differences were found:

- CWHvh1 restricted to exposed coasts yielded fewer occupied detections than the more inland CWHvm1 or vm2, but this was probably due to the negative effect of proximity to the ocean rather than differences in forest structure because some stands of CWHvh1 further inland on Flores Island yielded many occupied detections;
- CWHvm1 (found below 600 m) yielded more occupied detections than the higher, but similar CWHvm2, but this might have been an artefact of murrelets using low elevation flight corridors (Rodway and Regehr 2000) rather than differences in nesting density. Overall, detection frequencies and measures of suitable habitat were similar in valley bottoms and on lower slopes (<800 m), but were lower on the upper slopes (>800 m).

Significant differences among site series were found but these were less useful in identifying suitable habitat than the structural features of the forests. Rodway and Regehr (2002) concluded that structural characteristics (e.g., platform densities, large trees) were a better measure for identifying suitable habitat than detections from audio-visual surveys.

Also within Clayoquot Sound, a 4-year study of habitat associations was done in the Ursus Valley Special Management Area (Bahn 1998, Bahn et al. 1999, Bahn and Newsom 2000, 2002a,b). Although the methods differed somewhat with the overlapping analysis by Rodway and Regehr (2002), in general the results were similar (Table 4.10). One exception was that mountain hemlock and yellow cedar, both usually found at high elevations, showed significant negative associations with murrelets in the Ursus. Timber volume derived from timber inventory maps proved to be a useful proxy for mapping suitable habitat (see below). Significant differences were found among biogeoclimatic site series, but were accentuated when the site series were grouped into ecosystem productivity classes (Bahn et al. 1999). Productivity classes reflect the ability of the site to produce timber (Green and Klinka 1994: 197-216), and were more likely than site series to reflect meaningful forest structure and provide a mappable parameter.

Preliminary analysis of eight years of surveys in the Carmanah-Walbran (Burger and Bahn 2000) included controlling for the effects of visibility (canopy closure at the observation station). Occupied detections, primarily circling and subcanopy flights, were significantly correlated with known nest microhabitat indicators (availability of platform limbs, cover and thickness of

epiphytes, variable canopy structure), but total detections were not. The results shows many similarities with the Clayoquot data, but a few important differences (Table 4.10). Epiphyte cover was not significantly associated with high rates of occupied detections, although epiphyte thickness was. As in the Ursus Valley, biogeoclimatic site series grouped into productivity units (two for Carmanah-Walbran) were able to significantly separate stations with high and low occupied detection rates. Unlike the Ursus Valley, murrelet activities were not correlated with timber volume. Valley bottom stations had significantly higher values than slope stations for occupied and subcanopy detection rates. Although this was partly an artefact of better visibility at the valley bottom (Rodway and Regehr 2000), the negative correlation with elevation persisted even after visibility was statistically controlled (Table 4.10).

Coastal Douglas-fir (CDF) and dry western hemlock (CWHxm1) forests near Victoria were sampled in a two-year study (Burger et al. 2000b). Frequencies of detections and occupied detections were generally low compared to areas on the moister west coast of Vancouver Island. Comparisons were made between stations with or without occupied detections, and between those with or without any detections. Few significant associations were found with murrelet detections (Table 4.10), probably because stations were deliberately sited in apparently suitable habitat to maximise the chances of finding murrelets. The positive associations with distance from the ocean and elevation are likely artefacts caused by the paucity of old-growth remaining in low-lying coastal areas occupied by greater Victoria. All occupied detections and all but one station with any detections were in the inland Sooke Hills where the only extensive stands of old-growth remain, and three nests were found. Epiphyte cover and thickness, density of trees with platforms, and density of western hemlock showed weak, usually non-significant positive associations with detections. Biogeoclimatic site series grouped into productivity classes (Green and Klinka 1994) did not show any associations with murrelet occupancy or presence.

Habitat associations were studied in the Bunster Hills near Desolation Sound on the southern mainland coast (Manley 1999). In this area most of the low-lying forests have been logged and murrelets were nesting in the higher CWHvm2 and MH zones, usually in small remnant patches of old-growth. Occupied stands were between 600 and 1200 m in elevation, with most in the 701-900 m range. Data were usually analysed separately for each year, which sometimes yielded different results, and consequently some habitat features in Table 4.10 show more than one association score. Multiple regression analyses done separately for each year selected elevation, density of trees with platforms, and mossy platform scores as significant predictors of occupied detections, and mossy platforms, slope, elevation, tree age, and tree height (-ve), as predictors for total detections.

On Queen Charlotte Islands/Haida Gwaii, most studies have involved brief series of surveys to determine presence, occupancy and activity levels of murrelets in stands within timber harvest areas, but no quantitative habitat analysis. Three studies involved considerable habitat analysis and are reviewed in more detail here.

Rodway et al. (1993b) focused on Lagins Creek and Phantom Creek drainages with some sampling in other parts of Graham Island. Their study dealt mainly with vegetation site associations but also considered tree size and elevation (Table 4.10). The positive effect of

distance from the ocean was confined to the absence of murrelets along the coastal fringe where there was little epiphyte growth in the canopy. The highest levels of murrelet activity were associated with low elevation stands of Sitka spruce and western hemlock.

Materi et al. (1998) looked at a few habitat variables in forests surrounding Botany and Fairfax inlets. They subjectively assessed all the sampled habitat to have the qualities necessary for nesting, but stations near the coastal estuaries had lower frequencies of detections even though the habitat looked suitable. No complete statistical tests were made, but sites with low platform densities had few or no detections. There was a negative association between detections and epiphyte cover, probably due to the murrelet's avoidance of the trees bordering the estuary, which had high moss cover.

Dechesne and Smith (1997) did a comprehensive study over two years on NW Graham Island. Burger (1999) did some additional analyses with their data. Few significant habitat associations emerged from this study (Table 4.10). Murrelet detections and critical habitat measures were similar on the lower slopes and valley bottoms, but were lower in the small sample (three stations) on upper slopes and ridges.

Some additional short-term studies from BC are reviewed in Burger (1995b).

4.3.3 Conclusions on stand-level associations with murrelet activity

The results from these studies of murrelet detections and habitat associations were variable, involving different field measures and types of analysis, but some fairly consistent trends emerge (with emphasis on results from BC). Occupied detections and other measures of murrelet activity were generally positively associated with the following structural features:

- density of large trees (DBH >80 cm);
- tree diameter (DBH)
- variation in tree size (DBH or height)
- epiphyte cover on branches;
- epiphyte thickness;
- density of potential platforms per ha;
- density of trees with platforms.

and generally negatively associated with:

- elevation, and location within the valley, with valley bottom and lower slopes showing more occupied activity than upper slopes and ridges (although this might sometimes have been due to differences in visibility at the observation stations);
- forests on the fringe (<500 m) of exposed coasts.

High levels of occupied activity were usually associated with Sitka spruce, especially large trees of these species, and to a lesser extent western hemlock and amabilis fir. The associations with western red-cedar were mixed, but generally weakly negative. The two conifers often found at high elevations, yellow cedar and mountain hemlock, were negatively associated with murrelet detections, except for yellow cedars on the Sunshine Coast, where most nests were in this species (Manley 1999, Bradley and Cooke, unpubl.).

Table 4.10. Stand-level habitat associations based on audio-visual surveys of Marbled Murrelets in B.C.

Location	Clayoquot Sound	Ursus Valley, Clayoquot	Carmanah-Walbran
Reference	Rodway & Regehr 2002	Bahn et al. 1999	Burger & Bahn (unpubl.)
Biogeoclimatic zone or equivalent	CWH and MH	CWH and MH	CWH
No. of stations/sites	284	51	27
Years of study	3	3	8
MaMu measure	Frequency of occupied	Frequency of	Frequency of occupied
	detections (with / without	detections, occupied	detections, not
	controlling for factors	and subcanopy	controlled/controlled for
	affecting detections	detections	visibility
Macro-habitat parameters			
Distance from ocean	+*	NS	NS/-
Elevation	-*, especially >500m	_*	-*/-*
Slope		_*	
Aspect			
Distance from stream	NS (-)	_*	(-)
Recent logging near station	_*		
Stand area			
Stem density	NS	NS	NS/-*
Density of large trees (>80 cm dbh)	+*	+*	+*/NS
Tree age			_
Canopy closure	NS / +*	NS	_*
Timber volume	_	+*	NS/NS
Tree diameter (dbh)	+*	+*	+/+*
Variation in tree diameter	NS / +*	+*	+/+*
Tree height	NS / NS	+*	NS/+*
Variation in tree height	+* / NS	+*	+*/+*
Density of snags	NS / NS		
Tree characteristics			
Epiphyte cover on branches	NS / +*	+*	+/+
Epiphyte thickness		NS	+*/+
No. of potential platforms/tree			
No. of potential platforms/ha	+*	+*	+*/+
Density of trees with platforms	+*	+*	+*/+
Mistletoe score	NS		NS/NS
Associations with tree species	all / large	all / large	
Sitka Spruce	NS / NS	+* / +* (large)	+* / +
Western Hemlock	-* / + (large)	NS / +* (large)	- / -*
Mountain Hemlock	-* / -* (large)	-* / -* (large)	
Western Red-cedar	NS / NS	NS / NS (large)	-/-
Yellow Cedar	NS / NS	-* / -* (large)	
Amabilis Fir	+* / +* (large)	(+) / NS (large)	NS / NS
Grand fir			
Douglas-fir			

- + : positive association with MaMu
- : negative association with MaMu
 *: significant statistical test
- NS: not significant (statistical test)
- (+): +ve trend but no statistical test (-): -ve trend but no statistical test

Table 4.10 (continued). Stand-level habitat associations in B.C.

Location	SE Vancouver Island	Bunster Hills, s-central mainland coast	Graham Island, Haida Gwaii
Reference	Burger et al. 2000b	Manley 1999	Rodway et al. 1993b
Biogeoclimatic zone or equivalent	CDF & CWHxm	CWH and MH	CWH
No. of stations/sites	41	145	40
Years of study	1	3	1
MaMu measure	Comparing stations:	Comparing stations:	Frequency of detections
Maina measure	occupied vs. not	occupied vs. present vs.	r requeries or detections
	occupied; detections vs.		
	no detections	no detections	
Macro-habitat parameters			
Distance from ocean	+/+		(+)
Elevation	+*/+	-*	_*
Slope	NS	_*	
Aspect		NS	
Distance from stream	NS		
Recent logging near station	NS		(-)
Stand area	NS		
Stem density	NS	NS	
Density of large trees (>80 cm dbh)	NS/+* (>60 cm DBH)	NS	
Tree age		+*	
Canopy closure	NS		
Timber volume	NS		
Tree diameter (dbh)	NS	+* or (+)	+*
Variation in tree diameter	NS	NS	
Tree height	NS	NS	
Variation in tree height	NS		
Density of snags			
Tree characteristics			
Epiphyte cover on branches	+/+	+*	
Epiphyte thickness	+/+*	+*	
No. of potential platforms/tree	NS	NS	
No. of potential platforms/ha	NS	NS (+)	
Density of trees with platforms	NS/+	+* or (+)	
Mistletoe score	NS		
Associations with tree species			
Sitka Spruce			(+)
Western Hemlock	+*		(+)
Mountain Hemlock			
Western Red-cedar	NS	-* but had nests	(-)
Yellow Cedar		+* most nests	(-)
Amabilis Fir		_*	
Grand fir	-		
Douglas-fir	NS	_*	
<u> </u>	7		
Key: +: positive association with MaMu			
 - : negative association with MaMu 	1		

Key: + : positive association with MaMu
- : negative association with MaMu
* : significant statistical test
NS: not significant (statistical test)
(+) : +ve trend but no statistical test
(-) : -ve trend but no statistical test

Table 4.10 (continued). Stand-level habitat associations in B.C.

Location	Botany & Fairfax,	
	Haida Gwaii	Graham Island, Haida Gwaii
Reference	Materi et al. 1998	Dechesne & Smith 1997
Biogeoclimatic zone or equivalent	CWH	CWH
No. of stations/sites	66	27
Years of study	2	2
MaMu measure	Frequency of	Index of activity derived
Maina moddaro	detections &	from occupied detection
	occupied detections	frequency
Macro-habitat parameters		
Distance from ocean	(+)	
Elevation		_*
Slope		
Aspect		
Distance from stream		
Recent logging near station		(-)
,	(+)	
· · · ·		NS
•		
	()	
		NC
	(-)	
	(1)	NS
·		
· · · · · · · · · · · · · · · · · · ·		
	rare	
•	(+)	⊥*
	(+)	
		•
	(-)	(-)
	(-)	
		()
2009.00		
Key: +: positive association with MaMu]	
- : negative association with MaMu		
* : significant statistical test		
NS: not significant (statistical test)		
(+): +ve trend but no statistical test		
(-): -ve trend but no statistical test		
Stand area Stem density Density of large trees (>80 cm dbh) Tree age Canopy closure Timber volume Tree diameter (dbh) Variation in tree diameter Tree height Variation in tree height Density of snags Tree characteristics Epiphyte cover on branches Epiphyte thickness No. of potential platforms/tree No. of potential platforms/ha Density of trees with platforms Mistletoe score Associations with tree species Sitka Spruce Western Hemlock Mountain Hemlock Western Red-cedar Yellow Cedar Amabilis Fir Grand fir Douglas-fir Key: +: positive association with MaMu -: negative association with MaMu	(+) (-) (+) (+) (+) rare (+) (-)	(-) NS NS NS (-) (-) (-)

4.4 Associations between nest microhabitat features and stand-level macrohabitat features

Several microhabitat structures are consistently found at most tree nests (hereafter called *nest habitat indicators*: limbs or other structures forming platforms, epiphyte cover, large trees with variable canopy structure). Using these as indicators of suitable habitat allows useful comparisons with other habitat features, especially those that can be mapped. In some respects these microhabitat structures are a more objective measure of murrelet habitat than detections from audio-visual surveys, because they are not affected by weather, date, annual variations and station visibility (Rodway and Regehr 2000, 2002). Estimating the number of platforms from the ground can lead to errors, but these usually occur with high numbers of platforms and ground observers are fairly accurate at separating trees with or without platforms, or in estimating low numbers of platforms (Burger et al. 2000b, Rodway and Regehr 2000).

Associations between these nest habitat indicators and other habitat variables have been specifically analysed in the Ursus Valley (Bahn 1998, Bahn et al. 1999, Bahn and Newsom 2000, 2002 a,b), Clayoquot Sound as a whole (Chatwin et al. 2000, Rodway and Regehr 2002) and in Carmanah-Walbran (Burger and Bahn 2000, unpublished data), and a few similar comparisons were also available from the Nimpkish Valley, northern Vancouver Island (Harper et al. 2001 a,b,c) and the Sunshine Coast (Manley 1999). The five variables selected as important at murrelet nest sites were: density of potential platforms (large boughs); density of trees with platforms; epiphyte cover (in the Carmanah-Walbran sample epiphyte thickness was a better measure and was used instead of epiphyte cover); density of large trees (>80 cm DBH); and variability of the canopy structure, taken as the standard deviation of tree height or the standard deviation of DBH. These five variables were always positively associated with each other and usually significantly so (Table 4.11).

Macro-habitat variables useful for identifying and mapping murrelet habitat would be those that showed consistently positive or consistently negative associations with nest-site features, and ideally had statistically significant associations. A few macro-habitat variables emerge as important:

- elevation: this was negatively associated with nest features in the Clayoquot, Ursus and Carmanah-Walbran studies, but in the Nimpkish Valley the dry low elevation CWHxm2 and the highest MHmm1 subzones had fewer suitable features than mid-elevation CWHvm1 and vm2, and on the Sunshine Coast where most of the low-elevation forests had been logged there was a positive association with elevation and nest characteristics;
- location in the valley: stations in the valley bottom or lower slopes consistently had higher values for important nest features when logging had not biased the distribution of old growth forests;
- tree diameter (DBH): was consistently positively associated with nest features;
- tree height: usually positive, but less consistently so than diameter in the Carmanah-Walbran samples;

• biogeoclimatic site series grouped into productivity classes (Green and Klinka 1994): nest features were positively associated with high ecosystem productivity, whereas site series alone usually showed no significant associations.

Although stand age was not specifically tested in all these studies, it is strongly correlated with most of the structural variables identified here and should therefore be included too. Timber volume shown on timber supply maps was an important indicator in the Ursus Valley and used there for mapping (see below), but was not significantly associated with murrelet nest features in Carmanah-Walbran.

It is hard to draw strong conclusions from this relatively small sample, especially since all three detailed studies (Ursus, greater Clayoquot Sound, and Carmanah-Walbran) were done on the west coast of Vancouver Island and did not include all the habitat types used by murrelets in BC. A larger analysis involving more areas is obviously needed to test the relationships between nest microhabitat features important for murrelets and macrohabitat features suitable for mapping habitat and planning protected areas. Understanding these microhabitat-macrohabitat links will refine the criteria used in helicopter reconnaissance of potential WHAs, which is a rapid method for assessing habitat within timber management areas (Leigh-Spencer et al. 2002).

Table 4.11. Associations between nest-site micro-habitat and tree features and stand-level macro-habitat and biogeoclimatic features in British Columbia.

		Micro-habitat or tree features important at murrelet nests																						
	Poter	Potential platforms			Trees	Trees with platforms			Epiphyte cover				Dens	sity of	large	tree	S	Variable o	anopy	//tree	size			
	CQS	UR	CW	NV	SC	CQS	UR	CW	NV	SC	CQS	UR	CW	NV	SC	CQS	UR	CW	NV	SC	CQS UR	CW	NV	SC
Micro-habitat or tree features																								
Potential platforms							+*	+*				+*	+*				+	+*			+	+*		
Trees with platforms		+*	+*									+*	+*				+*	+*	+*		+	+*		
Epiphyte cover		+*	+*				+*	+*									+*	+			+*	+		
Density of large trees		+	+*	+*			+*	+*				+*	+								+*	+		
Variable canopy/tree size	+	+	+*				+	+*			+*	+*	+*				+*	+						
Macro-habitat features																								
Distance from ocean	+*	-	+			-	-	+			_*	-	-			-	+	+			+	+		
Elevation	-	-*	-		+	-*	-*	-			-*	_*	-*		+	_*	-*	_*	-*		_*	-		
Location in valley	+	+*				+*	+*	+*			+*	+*	+*			+*	+*				+*	+*		
Slope		-		NS			-					_*					-				-			
Stem density		+*	+				+	+				-*	-*				+*	-			_*	-*		
Canopy closure		+*	-				+	-				+	-*				-	+			-	-		
Timber volume		+*	+				+*	+				+*	-			+	+*	-			+*	-		
Tree diameter (dbh)	+	+	+	+*	+		+*	+		+	+*	+*	+*			+*	+*	+*	+		+*	+*		
Tree height	+*	+	-				+*	-			+*	+*	+*			+*	+*	+			+*	+*		
Associations with tree species																								
Sitka Spruce		+*		+*			+*					+*		NS			+*				+*			
Western Hemlock		+	+*	+*	-		+*	-				+	-	NS	-		+*	-		+	+	-		
Mountain Hemlock		-*		_*	-		-*					_*		-	-		_*			-	_*			
Western Red-cedar		-		NS	+		-					-*		NS	+		-			+	-			
Yellow Cedar		-*		_*	+		-*					_*		+	+		-*			+	_*			
Douglas-fir				+*	+									-	-					-				
Amabilis Fir		+*		+*	_		+*		+*			+		+			+			_				
Biogeoclimatic site-series	NS	NS		*	* ?	*	NS	*			*	*	NS	*	*	NS	NS		NS		NS	*		
Ecosystem productivity units		+					+	+*				+*	+		+						+*	+*		

Codes: CQS = Clayoquot Sound (Rodway & Regehr 2002, Bahn and Newsom 2002b); UR = Ursus Valley (Bahn 1998, Bahn et al. 1999, Bahn & Newsom in 2002b);

CW = Carmanah-Walbran (Burger & Bahn, unpubl.); NV = Nimpkish Valley (Harper et al. 2001 a,b,c); SC = Sunshine Coast (Manley 1999).

Key: + positive association; - negative association; * significant statistically; NS (or + and - without *) not significant statistically.

4.5 Landscape-level habitat associations

4.5.1 Large-scale analyses based on nests located by telemetry

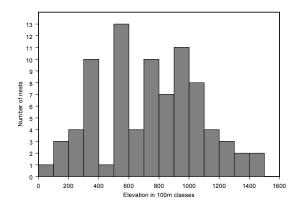
Desolation Sound (Sunshine Coast) - Analysis of murrelet nest sites located using radio-telemetry in the Desolation Sound area is still underway, and preliminary results are reported here (Huettmann et al., in prep.). The original authors should be consulted before citing any of the data summarised here.

This area has been intensively logged and is highly fragmented, both naturally and through logging (Manley 1999, Manley and Jones 2000). GIS data indicate that about 20% of the land area supports old-growth, and that patches of old-growth forest are usually small (median and mean forest patch sizes are 2.83 ha and 22 ha, respectively, range 0.002-3245 ha; Huettmann et al., in prep.). Areas below 400 m have been most intensively logged; they currently make up 36% of the land area, but only 16% the remaining old-growth forest (Huettmann et al., in prep.). Manley and Jones (2000) found that there was little habitat suitable for Marbled Murrelets in the low elevation biogeoclimatic subzones.

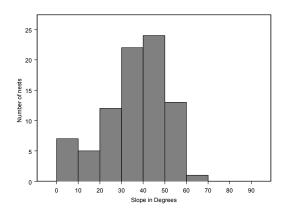
Stand-level analyses of the telemetry nest data (Waterhouse et al. 2002) are reported in section 4.3.1. On the larger landscape scale, Huettmann et al. (in prep.) compared the habitats at nest sites with habitat at randomly selected points within the 50 km radius of the Desolation Sound capture site. This area included 81of 84 nest sites located by telemetry. The positions of nest sites were located in the field using GPS (precision ~30 m), and compared with habitat data derived from GIS sources, focusing on the effects of elevation, slope and aspect. To compensate for the spatial inaccuracy in some of the GIS data, Huettmann et al. (in prep.) added 100 m buffer zones around forest polygons. Sixty nests fell within forested polygons or in the 100 m buffer zone and were compared with a similar number of randomly-selected forested sites.

Old-growth (>140 years old) made up 20% of the land within the 50 km circle, and most of the remaining area had been logged in the past 140 years. Most of the existing old-growth was between 800-1000 m in elevation, and on slopes of 20-50 degrees. Elevation and slope were significantly positively correlated in this area. The mean elevation of nests was 748 ± 350 (SE) m (range 38-1530 m) and the mean slope was 36 ± 15 degrees (range $0-61^{\circ}$)(Figure 4.1). [Note that slopes are presented as degrees throughout this review although reported as % in some studies]. Nests were found on slopes with all aspects, with slightly more facing north and east (Figure 4.1).

A) Elevation



B) Slope



C) Aspect

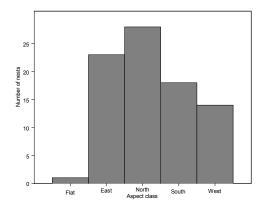


Figure 4.1. Distribution of Marbled Murrelet nests in Desolation Sound located by radio-telemetry, showing the frequency of nests relative to elevation (A), slope (B), and aspect C). From Huettmann et al. (in prep.).

To compensate for the skewed distribution of old-growth forest, relative to elevation and slope categories, the distribution of nests was plotted as the numbers of nests per 1000 ha of forest habitat within each elevation and slope category (Figure 4.2), using the data from Huettmann et al. (in prep.). This analysis shows few nests, relative to forest area, below 200 m, a peak in relative density at 200-400 m with a gradual decline with increasing elevation above 400 m. The distribution relative to slope shows a small peak in relatively flat ground (<10 degrees slope), with a large peak centred on steep slopes of 40-70 degrees.

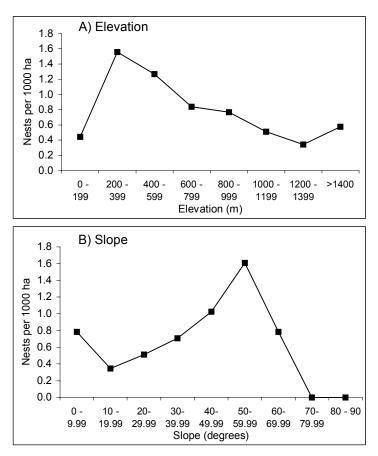


Figure 4.2. Distribution of the Desolation Sound telemetry nests plotted by elevation (A) and slope (B), taking into account the proportion of forest habitat in each elevation and slope category. Data were plotted as nests per 1000 ha of forest habitat in each elevation or slope category using data from Huettmann et al. (in prep.).

Huettmann et al. (in prep.) dealt with the skewed distribution of elevation, slope and aspect by comparing the nest-site habitat with habitat from randomly selected points, and incorporating these within multivariate models. To account for sampling variability in the landscape they conducted the analysis 1000 times, using distinct sets of randomly drawn locations. They then identified the models that were selected most often in these 1000 iterations. In analyses considering all land areas (not only forested land), the two most successful models included:

- Slope (+ve effect) x Slope² (-ve) x Elevation² (+ve) (selected 228 times);
- 10 combinations of Slope, Elevation and Aspect (selected 115 times).

In analyses that considered only old-growth forest, the two most successful models included:

- Slope (+ve effect) (selected 118 times)
- Slope (+ve) x Elevation² (-ve) (selected 114 times).

The actual coefficients for slope and elevation generated by these models are given in Huettmann et al. (in prep.).

Overall, slope had a strong positive effect (more nests with increasing slope), elevation a less consistent effect (+ve in some models and –ve in others), and aspect was seldom selected as significant. The combined effects of elevation and slope on the predicted distribution of murrelet nests in Desolation Sound is shown in Figure 4.3. Huettmann et al. (in prep.) also found that nests were less accessible to people on the ground on steeper slopes and at higher elevations.

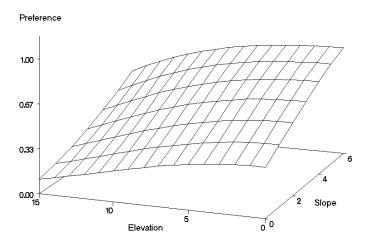


Figure 4.3. Model outcome predicting the influence of elevation (in 100 m intervals from 0-1500 m), and slope (in 10 degree intervals from 0-60 degrees) on nest distribution of Marbled Murrelets in Desolation Sound (from Huettmann et al., in prep.).

Huettmann et al. (in prep.) also found that nesting success to the mid-chick stage could be modeled by elevation and slope. Nest success tended to increase with increasing elevation and increasing slope (Figure 4.4).

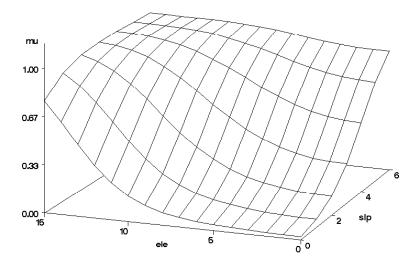


Figure 4.4. Model predicting nesting success to mid-chick stage of Marbled Murrelets in Desolation Sound, relative to elevation (in 100 m intervals from 0-1500 m), and slope (in 10 degree intervals from 0-60 degrees). From Huettmann et al., (in prep.).

Using GIS data Huettmann et al. (in prep.) also investigated the distribution of nests relative to forest patch size (measured from GIS forest maps on a 1:20,000 scale). Patches of old-growth less than 200 ha in area made up 95% of the available patches, 48.6% of the old-growth area, and contained 60% of the 50 nests within polygons classified as old-growth. An additional 31 nests were in polygons not classified as old-growth, suggesting that they were in small forest patches (<50 ha) in habitat classified as old-growth/scrub. Overall, these data indicate that most nests in Desolation Sound were in small old-growth patches.

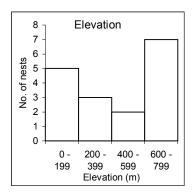
Using the same sample of nests, Bradley (2002) found significant correlations between the timing of breeding, commuting distance between nests and feeding areas, and the slope and elevation at nest sites. Timing of breeding was significantly negatively correlated with commuting distance. Slope at nest-sites was significantly negatively correlated with timing of breeding, and positively with commuting distance. All of these correlation coefficients were, however, relatively small (The correlation coefficients between timing of breeding and commuting distance were about twice those between slope and commuting distance). Elevation was not significantly correlated with commuting distance or timing of breeding, and slope and elevation were positively correlated in one of three years. Overall, it appeared that early nesting murrelets tended to travel further from foraging areas to nest, and nested in steeper slopes than those nesting later.

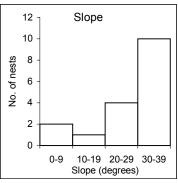
Using univariate logistic regression models to study nesting success, Bradley (2002) found that early-breeding birds were more successful, and success increased with increasing commuting distance, slope and elevation. There were no apparent variations among years in these patterns. Multivariate analyses combining these intercorrelated variables, including stepwise models, did not resolve which was the dominant effect. Reduced predation at nests further inland and at higher elevations was suggested as a possible explanation for these patterns (Bradley 2002). Distribution of these nests relative to forest edges is summarised in section 4.7.2.

Central Mainland Coast - Kaiser and Keddie (1999) located 12 nest sites on the central mainland coast by tracking birds caught in Mussel Inlet (Mathieson Channel). This area typically has high, steep, glaciated valleys and slopes. There has been relatively little logging of old-growth. Descriptions of the nest sites were restricted to aerial observations and with reference to maps, and the precision of locating the nests was low (ca. 100 m), leading to some uncertainty in matching aerial photographs with GPS locations (L. Waterhouse, pers. comm.). The 12 nest sites had a mean elevation of 375 m (SD = 201 m, range 110-800 m), were on relatively steep slopes, averaging 50 degrees (SD = 16°, range 30-70°), and averaged 5.5 km from the sea (SD = 6.0 km, range <0.5-18 km). The nests were on slopes with NE aspect (4 nests), SE (4), S (2), N (1) and E (1). One nest was on the ground on a steep rock face with shrubs (see Bradley and Cooke 2001), and the others were evidently in trees.

Kaiser and Keddie (1999) compared the habitat characteristics of the Mussel Inlet catchment (East Quadrat, 40,000 ha) in which all 12 nests were found with the nearby lowland old growth forest between Bollin Bay and Green Inlet (West Quadrat, 6000 ha) in which no nests were found. The East Quadrat included higher proportions of land which were classified as high elevation (e.g., 97% above 300 m), alpine or Mountain Hemlock Biogeoclimatic Zone, smaller trees, and low tree growth index, and lower proportions of Coastal Western Hemlock Biogeoclimatic Zone, larger trees, and high tree growth index. Only 10% of the East Quadrant land fell within areas rated as moderate to excellent on a Marbled Murrelet Suitability index (source of the index not given), compared to 55% in the West Quadrat. These preliminary results should not be interpreted to mean avoidance of the West Quadrat lowland islands by murrelets, because Schroeder et al. (1999) reported hundreds of murrelets entering watersheds on these islands. If one considers the distribution of nests relative to the availability of forest in the East Quadrat, where all the nests were found, areas below 300 m made up only 3% of the forest area, but contained 42% of the nests (Kaiser and Keddie 1999). Areas below 1000 m made up 34% of the forested area but contained all the nests. This small sample shows that murrelets will nest in sub-alpine areas, but use lower elevations disproportionately even when the forests there are sparse. The use of steep slopes is consistent with the results from Desolation Sound (Huettmann et al., in prep.).

Clayoquot Sound – Telemetry studies were done by the SFU Wildlife Ecology Chair group in 2000 and 2001. The study is not complete and only preliminary results are available from 17 nests (Figure 4.5). Relative to the Desolation Sound sample, the murrelet nests were in lower elevations. All nests were below 800 m, and 59% below 600 m. Similarly, although there was a tendency to nest on slopes, rather than flat ground, the slopes used were less steep than in Desolation Sound and Mussel Inlet. Nests were on slopes of all aspects, with fewer facing west. There are no detailed data yet to compare the distribution of these nests relative the availability of habitat, but a rough analysis of elevation is possible using the areas of biogeoclimatic subzones (Burger 2001). Zones 0-600 (CWHvh1 and vm1), 600-900 (CWHvm2) and 900-1300 m (MHmm1) in elevation made up 56%, 32%, and 12%, respectively, of the available mature forest around Clayoquot Sound, and contained 59%, 41% and 0% of the nests, respectively. This preliminary analysis suggests approximately equal distribution of nests, relative to available habitat, below 900 m, and no evidence of nests in the forests above 900 m.





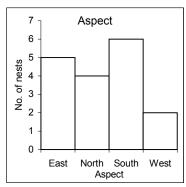


Figure 4.5. Distribution of nests found by radio-telemetry in Clayoquot Sound, relative to elevation, slope and aspect. Unpublished data from F. Huettmann and Wildlife Ecology Chair, Simon FraserUniversity.

Queen Charlotte Islands/Haida Gwaii - Radio-telemetry was used to track murrelets and find nests in 2000 (Manley et al. 2001). Seven nest sites were identified but none of the nest trees was found. Nesting areas were close to the shore, ranging from 25 m to 4.2 km inland, with three sites within 300 m of the shore. Mean elevation was 219 m (SD = 197 m, range 0-460 m, and mean slope was 30 degrees (SD = 15°, range 0-40°). Forest age was available for 6 nests, and 3 were in each of class 8 (141-250 years) and class 9 (>250 years). Three sites fell into tree height classes 3 (19.5-28.4 m), two in class 4 (28.5-37.4 m) and one in class 5 (37.5-46.4 m). Densities of potential nest platforms measured within the nest stands averaged 126 platforms per ha (SD = 45, range 53-182). These nest sites were used to test the McLennan et al. (2000) habitat suitability algorithm (see section 4.6.2).

4.5.2 Large-scale analyses using audio-visual detection data

A broad-scale pilot study covering 82 watersheds on Vancouver Island was done in 1991 by Savard and Lemon (1994). Although the sampling effort per watershed was sparse and the methodology variable, some patterns emerged. Distance from the coast did not have a consistent effect on detection rates. Watersheds with less than 50% of their forested area in old-growth yielded fewer detections than watersheds with more old-growth, and stations within 500 m of old-growth stands had significantly more detections than those further from old-growth. Watersheds on the west coast of the island had higher mean detection rates than those on the east coast. The lowest detection rates were in the Georgia Depression Ecoprovince on the southeastern side of Vancouver Island. These results were confirmed by more intensive recent work, showing that the rates of detections and occupied detections in the Coastal Douglas-fir forests (CDF and associated CWHxm1 biogeoclimatic zones) near Victoria were 4-8 times lower than corresponding measures on the west coast in Carmanah-Walbran and Clayoquot Sound (Burger et al. 2000b). These differences are likely the effects of climate (the west coast is more moist than the east coast), and logging (very little old-growth remains on the east coast but there still are large tracts on the west coast). Differences in marine habitat quality might also be involved, but are not known.

A similar large-scale study was done on Haida-Gwaii in 1990 by Rodway et al. (1991, 1993a,b). The number of detections was higher in old-growth forests than in alpine areas. Differences with elevation in the Lagins Creek watershed were also found: detection rates per survey at low elevation forests (90-150 m), high forests (230-460 m) and alpine areas (720-1000 m) were 32 ± 4.1 (SE), 17.5 ± 3.0 and 3.0 ± 0.7 , respectively (Rodway et al. 1993b). There was no evidence of nesting in alpine areas. Likewise, Eisenhawer and Reimchen (1990) found no evidence of Marbled Murrelets in high elevation (>700 m) subalpine forest of lodgepole pine (*Pinus contorta*) above Coates Lake, Queen Charlotte Islands/Haida Gwaii, but found considerable activity associated with old-growth forests.

Using detection and habitat data gathered over two years from three watersheds on southwest Vancouver Island (Walbran, Carmanah and Klanawa watersheds), Burger et al. (2000a) found that shoreline strip forests (<250 m inland) represent suboptimal habitat for murrelets, compared with adjacent interior forest. Murrelet detections, including occupied and subcanopy behaviors, were significantly lower at 30 coastal stations (20-250 m from the shoreline edge) than at 30 interior stations (1.5-21.0 km inland). Densities of predators were significantly higher at the coastal stations. The coastal trees were of similar mean height and diameter, but they had lower structural diversity and provided fewer and less suitable (thinner epiphyte cover on large boughs) nesting platforms than trees in the interior. It was not possible to determine from these data how far inland the coastal effects penetrated. Elsewhere on Vancouver Island, in Clayoquot Sound, Rodway and Regehr (2002) found significantly fewer occupied detections near ocean edges than farther inland. In Washington, Hamer (1995) observed no evidence of occupancy by murrelets within 800 m of the coast even though the vegetation characteristics indicated excellent habitat. Burger et al. (2000a) concluded that where possible reserves for Marbled Murrelets should be placed in interior and not shoreline forests. Recent telemetry studies have, however, confirmed that murrelets do nest close to the shore. Three of 12 nest sites found by Keddie and Kaiser (1999) in Mussel Inlet, and 3 of 7 sites found by Manley et al. (2001) in the Queen Charlotte Islands/Haida Gwaii were within 0.5 km of shore. The effect of proximity to shore on nesting success is not known.

Several studies have examined landscape-level relationships outside BC. In Washington 98% of all detections occurred within 63 km of the ocean and below 1067 m elevation, with rapid dropoffs in detections beyond these points (Hamer 1995). In this state little old-growth forest remains on the coastal lowlands, and the remaining murrelet habitat might be less optimal, in inland hills and mountains. Raphael et al. (1995) considered landscape-level habitat associations in western Washington using GIS data, including satellite imagery. From audio-visual ground surveys, they grouped 261 stations into three classes: those with occupied detections; those with detections but not occupancy; and those without detections. These three categories did not differ in their distance from the ocean (mean 30.6 km) or elevation (mean 482 m, 0-1455 m), but differed significantly in the proportions of old-growth forest in the 203 ha surrounding each station. In general there was little old-growth in the sample area (mean <15%). Stations showing occupancy had more old-growth and large trees (sawtimber) in their neighbourhood than those with no occupancy. Occupied sites also had more complex landscape patterns, with more edge, more variable cover types, and more complex shapes. Variables that best discriminated among the three detection categories were proportion of old-growth, landscape-pattern index, old-growth

stand size, large sawtimber proportion and large sawtimber shape index. Even though these measures differed significantly among the three site classes, the overall discrimination function was able to correctly classify only 44% of the sites. This study included highly fragmented and depleted habitat (stand size range 44-203 ha) which is not typical for much of British Columbia.

Meyer and Miller (2002) used logistic regression to compare plots which had evidence of murrelet occupancy with those with no occupancy following intensive audio-visual surveys (4033 surveys at 3609 stations) in the fog-influenced coastal forests of northern California and southern Oregon. Habitat associations were tested at spatial scales of 400, 800, 1600 and 3200 m radii, and the two larger scales showed the strongest relationships with murrelet occupancy. Murrelets were most strongly associated with low-elevation unfragmented old-growth forests. They stressed the need for large, contiguous blocks of old-growth forest, preferably within a matrix of larger, more mature second-growth forest.

4.5.3 Watershed-level analyses using radar and GIS

Murrelets entering a watershed can be counted using a marine surveillance radar positioned at the watershed mouth. This is presently the only way to estimate numbers of murrelets using landscape-level areas. The method has been widely tested in several studies and the advantages and limitations are becoming well documented (Cooper et al. 1991, 2001; Hamer et al. 1995; Burger 1997, 2001, 2002; Cooper and Hamer 2000). Radar counts provide minimum estimates of the actual numbers entering watersheds because some birds are always likely to be missed and flock sizes are underestimated. Breeders and non-breeders cannot be distinguished. Murrelets sometimes cross from one watershed to another, so that counts at the watershed mouth do not always reflect the numbers remaining within that watershed. This error can be minimised by considering watersheds bounded by high mountains, or by modifying the catchment area by considering likely flight paths relative to local topography (Burger 2001, 2002, Raphael et al. 2002).

In addition to providing estimates of the number of murrelets using each watershed, the radar counts can also be compared with habitat measures within the watersheds using Geographic Information Systems (GIS) to determine landscape-scale habitat associations (Burger 2001, Raphael et al. 2002). Such analyses also reveal some of the impacts of logging on murrelet populations. In particular they address one of the most important conservation and management questions: How do populations of murrelets respond to reductions in the areas of old-growth forests? There are two alternative hypotheses explaining how murrelets might respond:

H1: Watershed populations decline in proportion to the reduction of old-growth forest (i.e., the birds do not pack into remaining patches of old-growth in higher densities). H2: Watershed populations remain relatively constant despite some loss of old-growth (i.e., the birds nest at higher densities in the remaining suitable habitat).

The radar data can be used to test these hypotheses in three ways. First, if murrelet numbers are correlated with area of existing forest, taking into account reductions, this supports H1. If murrelets were packing into reduced habitat in higher densities this would skew the correlation with existing habitat and logged watersheds should show higher numbers of murrelets per area of

existing habitat. Second, logging effects might be shown more directly by comparing numbers of murrelets per watershed relative to the areas of original and remaining old-growth. Reduced numbers of murrelets, relative to areas of original forest, in watersheds which have been heavily logged will support H1, but no decline will support H2. A third approach is to track the changes in the number of murrelets over many years as logging takes place in a sample of watersheds, with controls in un-logged watersheds. Data are available for the first two analyses, but not the third.

Relationships between murrelet counts and areas of existing habitat – Five independent studies from BC and one from the Olympic Peninsula, Washington (Raphael et al. 2002) provide data for testing relationships. The BC data were from Clayoquot Sound (Burger 2001, 2002), northwest Vancouver Island (Manley 2000, unpublished data), the Sunshine Coast on the southern mainland (Cullen 2002), Central Mainland Coast (Schroeder et al. 1999), and the Northern Mainland Coast (Steventon and Holmes 2002). All the studies reported significant correlations between the numbers of murrelets entering watersheds and existing areas of suitable nest habitat, defined in various ways (details below). Correlations do not necessarily imply causal relationships, but there are some consistent patterns among the studies which point towards functional links between habitat and murrelet numbers.

The BC radar data are summarised in Appendix 3. As part of this review the data were subjected to additional analysis to test the nature of habitat relationships and determine murrelet densities. Outliers which could be excluded on biological reasons were omitted and the data from each study were subjected to curve-fitting tests. In each study area there were significant relationships between murrelets and habitat area. Power equations (i.e., murrelet number = a x habitat area where a is a constant and b is the exponent) and linear regressions provided the best fits. Examples using the 'most likely habitat' from each study (see Appendix 3) are shown in Figure 4.6.

A power function gives a curvilinear relationship, typically showing a gradually reduced slope with higher values of the independent variable. In this case, when the number of birds (dependent variable) is plotted against the area of habitat (dependent variable), the slope (density of birds per ha) would decrease gradually with increasing habitat area. A strong power function would therefore indicate lower densities for larger areas of habitat. Such a trend is evident for the Central Coast and the North Coast, but was not found for the other three study areas (Figure 4.6). For Clayoquot Sound and NW Vancouver Island, the power and linear regressions were virtually identical (Figure 4.6), and had similar abilities to predict the trend. The situation is less clear for the Sunshine Coast, where the two curves give somewhat different trend lines but both gave highly significant R² values (Figure 4.6).

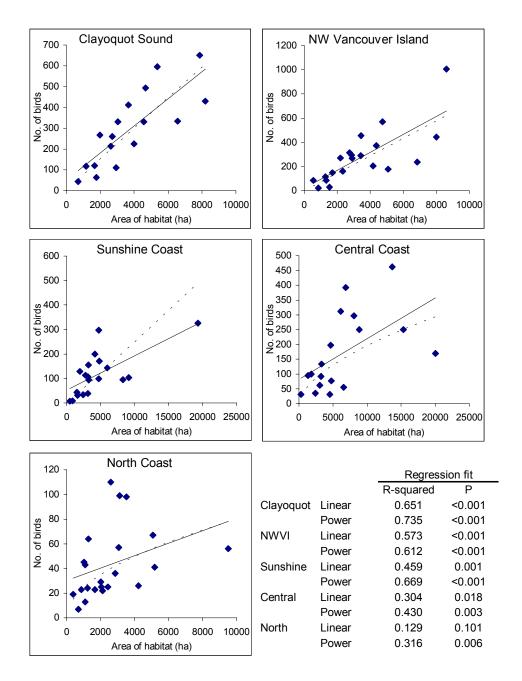


Figure 4.6. Comparison of linear (solid line) and power (dotted line) regressions for the relationship between murrelet counts made with radar and areas of habitat in five study areas in BC (data in Appendix 3). Each point represents data from one watershed. In each plot the habitat area is the "most likely" habitat as defined in Appendix 3. Note that the axes have different scales in each graph.

All of the BC studies showed considerable scatter of data points. Some of the variability in the data was removed by the exclusion of obvious outliers, but much remains in all the data sets. There are several sources of variability in radar counts, including the effects of weather (slightly higher counts on cloudy or foggy days), and seasonal and inter-year variations (Burger 1997, 2001, Cooper et al. 2001). These factors become relevant when a watershed is sampled only

once, providing no opportunity to ameliorate these causes of variability by averaging results from several surveys. Furthermore, several surveys are sometimes required to clearly identify the flight-paths that murrelets are using, and therefore make an accurate count. Repeated sampling of each watershed over several years is likely to greatly reduce the variability. This is evident in the Clayoquot Sound study, which sampled each station at least twice per season for 2-3 years, and provided much clearer patterns than the other studies which had less sampling effort.

An additional source of error comes in matching the count of murrelets with the appropriate area of habitat. Murrelets are known to cross from one watershed to another across hills and mountain passes, and it is virtually impossible to accurately estimate the number of birds that does so. In the Clayoquot Sound and NW Vancouver Island studies some adjustments were made (combining or splitting watersheds) where there was evidence of inter-valley movements (Burger 2001, 2002, Manley 2000 and unpubl.). Such adjustments might partially explain the generally stronger correlations found between murrelets and habitats in these two studies compared with the other three.

The fact that significant density trends emerged from all five studies, despite the low sampling intensity and multiple sources of variability, suggests that there are some strong underlying biological processes involved. This gives some confidence that useful trends and density estimates applicable for management should emerge from radar counts coupled with GIS data.

Habitat associations and effects of logging in each radar study – Habitat associations in Clayoquot Sound (Burger 2001, 2002) and northwest Vancouver Island (Manley 2000) were very similar (Table 4.12). In both areas several habitat measures were significantly correlated with murrelet counts, but some of these were intercorrelated and also significantly correlated with the total area of watersheds. With the data controlled for total watershed area, significant partial correlations remained with areas of mature forest (effectively mostly old-growth) and especially area of mature forest below 600 m (Table 4.12). In Clayoquot Sound there were also significant negative correlations with the areas of areas of logged and immature forest, but this was less evident in northwest Vancouver Island. Both studies suggest that the strongest associations were with low elevation old-growth forests.

Table 4.12. Correlations between murrelet counts per watershed made with radar and landscape-level habitat parameters in 18 watersheds in Clayoquot Sound (CQS; Burger 2001) and 20 watersheds on NW Vancouver Island (NWVI; Manley 2000).

Uncontrolled	Controlled for	Uncontrolled	Controlledfor
	total area	O noon to one a	Controlled for total area
Pearson		Pearson	Partial
correlation	correlation	correlation	correlation
0.704**	-	0.631**	-
0.323	0.004	-	-
-0.196	-0.757**	-0.098	-0.309
-0.323	-0.646**	0.404	-0.304
-0.344	-0.862**	0.383	-0.355
0.822**	0.845**	0.682**	0.450*
0.713**	0.160		
0.824**	0.620**	0.838**	0.739**
0.677**	-0.008	0.439	-0.774**
0.560*	-0.158	0.377	-0.214
-0.415	-0.204	0.596**	0.725**
0.850**	0.674**	0.534*	-0.166
0.686**	0.084	0.489*	-0.765**
0.511*	-0.271	0.197	-0.520*
	0.704** 0.323 -0.196 -0.323 -0.344 0.822** 0.713** 0.824** 0.677** 0.560* -0.415 0.850** 0.686**	Pearson correlation Partial correlation 0.704** - 0.323 0.004 -0.196 -0.757** -0.323 -0.646** -0.344 -0.862** 0.822** 0.845** 0.713** 0.160 0.824** 0.620** 0.677** -0.008 0.560* -0.158 -0.415 -0.204 0.850** 0.674** 0.686** 0.084	Pearson correlation Partial correlation Pearson correlation 0.704** - 0.631** 0.323 0.004 - -0.196 -0.757** -0.098 -0.323 -0.646** 0.404 -0.344 -0.862** 0.383 0.822** 0.845** 0.682** 0.713** 0.160 0.838** 0.677** -0.008 0.439 0.560* -0.158 0.377 -0.415 -0.204 0.596** 0.850** 0.674** 0.534* 0.686** 0.084 0.489*

^{*}P<0.05, **P<0.01

The Clayoquot Sound radar data showed the effects of logging. Five of the 18 watersheds had been relatively heavily logged (17-35% of original old-growth removed, most of it in valley bottoms), whereas 6 had experienced minor logging (<10%) and 7 had no logging. When murrelet numbers were plotted against area of original forest (which included mature, immature and logged areas), three of the five heavily logged valleys (Kennedy, Bedwell and Cypre) had far fewer murrelets compared with linear trend seen in the other watersheds (Figure 4.7A). When plotted against the areas of existing low-elevation forest (<600 m), these deviations disappeared (Figure 4.7B), but the deviations remained if all existing mature forest at all elevations or existing high elevation forest (>600 m) were considered (Burger 2001).

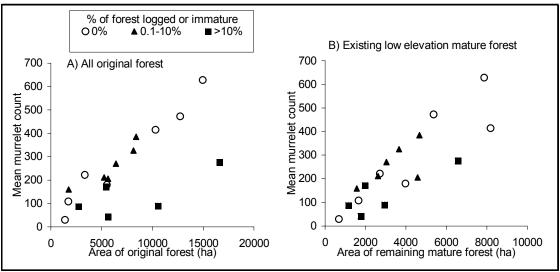


Figure 4.7. Relationships between annual mean counts of Marbled Murrelets and areas of original forest, including forest now logged or immature (A), and areas of existing low elevation old-growth (B) in Clayoquot Sound (Burger 2001).

These data support H1 and reject H2. In three of the five heavily logged valleys the numbers of murrelets had declined and there was no evidence that they packed into remaining habitat in higher densities. In contrast, densities (birds per habitat area) were more uniform when existing low elevation forest was considered, although a scatter of data points remained.

Manley (2000) investigated the effects of logging by comparing the densities of murrelets (birds per ha of existing old-growth) in watersheds with varying amounts of logging. Densities based on area of existing habitat were consistent across five regions on northwest Vancouver Island and were not correlated with the amount of remaining forest or the amount of habitat loss due to logging (Manley 2000). The murrelets were evidently not packing into remaining forest in harvested watersheds in higher densities, thus supporting H1 and not H2.

Schroeder et al. (1999) also did radar counts at 22 watersheds on the central mainland coast of BC in 1998. They derived habitat data from two sources: Broad Ecosystem Unit (BEU) inventory, which is based on biogeoclimatic ecosections and subzones reflecting a range of soil, terrain, forest cover and topographic features (RIC 1998a); and Forest Cover maps in which dominant species, tree height and age classes were derived from interpretations of aerial photographs.

Using the BEU database, habitat polygons were ranked from 1 (Highly Suitable) through 6 (No suitability, successional stages), based on forest age, the dominance of tree species likely to support murrelet platforms (e.g., Sitka spruce and western hemlock ranked high, deciduous species and mountain hemlock ranked low), and slope (steeper slopes ranked lower than valley bottoms). Mapped polygons containing more than one Broad Ecosystem Unit were ranked by weighting the proportions of each unit if they exceeded 25%. When suitable habitat was defined as including the top 3 ranks, there was a positive but not significant relationship between murrelet numbers and suitable habitat area ($r^2 = 0.14$, df = 21, P = 0.08), but when only the top two ranks of habitat were considered the relationship was positive and significant ($r^2 = 0.23$, df =

21, P = 0.02). There were no differences in these comparisons between valleys with recent logging and un-logged valleys.

Using the Forest Cover data, Schroeder et al. (1999) classified suitable habitat on the basis of the Identified Wildlife Management Strategy (IWMS) requirements for Marbled Murrelets (Anon. 1999). Suitable habitat included all areas with tree age class 8 or higher (>141 years), and height class 4 and above (>28.5 m). With all 22 watersheds included, they found no significant relationship between murrelet numbers and areas of suitable habitat (P > 0.1). When 9 logged and 13 un-logged valleys were treated separately, the former showed no relationship between murrelet numbers and area of suitable habitat (P = 0.04, df = 8, P > 0.1), but the latter showed a positive relationship (P = 0.24, df = 12, P = 0.08), although this was not statistically significant in either case. The failure of the suitability criteria to predict murrelet numbers in this test is not entirely surprising, given that many of the nests found in highly modified landscapes in the southern part of this coast (Desolation Sound) were in trees and forest stands which fell outside the suitability thresholds set by the IWMS requirements (Manley 1999, F. Cooke unpubl. data). In addition, counts made by Schroeder et al. (1999) showed several outliers (Appendix 3). When these were excluded on biological grounds significant trends were more obvious (Figure 4.6).

Drever and Kaiser (1999) also compared radar counts with habitat measures at 15 sites on the central mainland coast, but used somewhat different methods than those in the other radar studies reviewed here. Radar stations were placed at constrictions and mouths of inlets, rather than at mouths of discrete watersheds, and they therefore sometimes counted murrelets entering several watersheds. Habitat variables for each 'catchment area' were derived from GIS data (Biogeoclimatic Ecosystem Classification, Baseline Thematic Mapping, and Regional Forest Cover maps) for all watersheds that had some part within 15 km of the ocean. Multiple regression analyses selected areas of fir species (Abies spp.), alpine habitat and areas with slopes of 0-30° as significantly correlated with mean dawn counts (explaining 61%, 11% and 8% of the variability in mean counts, respectively, and 80% overall). Maximum dawn counts were best explained by areas of fir (55%) and hemlock (9%), and a negative correlation with areas between 0 and 300 m elevation (11%). Drever and Kaiser (1999) found that none of the variables traditionally viewed as measures of good habitat were correlated with murrelet counts, but did not explain the absence of these variables in their correlations. These variables included: areas with tree height class 4 (28.5-37.4 m) or class 5 and above (>37.5 m); structure stage and age class rated excellent (age class >9 [>250 years] if tree height class =5) or good (age class 9 if tree class 4); timber volume high (601-900 m³/ha); and site index (an index of forest site quality combining age and height) of 15 m or 20+ m (the highest two categories).

Cullen (2002) compared murrelet counts from 2000 and 2001 with habitat measures at 21 watersheds on the Sunshine Coast, southern mainland. Habitat was classified using biogeoclimatic zones, elevation, forest age, and tree size. Radar counts were most strongly correlated with the areas of old forest (>250 years) in both high (>650 m) and low (<650 m) biogeoclimatic zones (partial correlation, r = 0.630, P<0.01, controlled for total watershed area). Other combinations of old forest and large trees gave similar results regardless of elevation. Counts were negatively correlated with areas of alpine tundra and with areas of mature (140-250 m).

year old) forest. Evidently the birds were responding to areas of old (>250 years) but not mature (>140 years) forest.

Steventon and Holmes (2002) did a preliminary analysis of radar counts made in 2001 and habitat at 26 watersheds on the northern mainland coast of BC. Simple correlations suggested positive correlations of murrelet numbers with areas of old forest and negative correlations with slope and elevation. They also found a significant positive relationship between murrelet densities and the quality of habitat in each watershed derived from a Habitat Suitability Index model which incorporated % slope, % edge, canopy closure, forest age, tree height class, and elevation.

Raphael et al. (2002) compared radar counts of murrelets with habitat variables derived from satellite imagery in 10 large watersheds on the Olympic Peninsula. They concluded that radarbased counts could be a sensitive indicator of habitat conditions at the landscape level. The maximum number of murrelet radar targets was positively correlated with the areas of late-seral (i.e., old-growth) habitat below 1067 m elevation in each of three years (correlation coefficient 0.83-0.91, P<0.01), and this pattern was maintained in two of the three years when controlling for the size of the watershed (Figure 4.8). They also tested for patch size and edge-effects. Counts increased significantly as the amount of core-area old-growth (defined as interior forest >100 m from an edge) increased, but decreased with increasing amounts of edge in late-seral patches. Numbers of murrelets were not correlated with the percent of late-seral habitat, patch density (number of patches per ha), mean patch size, or spacing (proximity) of late-seral patches, nor with the overall diversity of all habitat types within the landscape. Although these data do not allow a direct test of the effects of logging on murrelet numbers, the correlation with existing areas of old-growth support H1 rather than H2.

In summary, significant correlations were found between counts of Marbled Murrelets made with radar and inland areas of forest habitat in all of the studies reviewed. The trends were most obvious in studies where there had been multiple years of surveys (Clayoquot Sound, northwest Vancouver Island, Sunshine Coast and Olympic Peninsula). Available areas of low elevation forest were good predictors of murrelet counts on the west of Vancouver Island and Olympic Peninsula (uncorrected correlation coefficients ranged from 0.82 to 0.91), but elevation was less important on the Sunshine Coast where much of the low elevation old-growth has been logged. Several studies showed evidence that logging of portions of the watershed had a detrimental effect on murrelet numbers, suggesting that murrelets did not pack into the reduced habitat in higher densities.

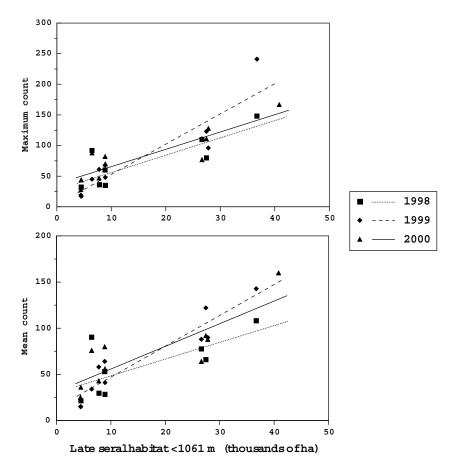


Figure 4.8. Associations between numbers of inbound murrelet radar targets and amount of late-seral coniferous forest below 1067 m (potential nesting habitat) for drainages on the Olympic Peninsula, 1998-2000 (Raphael et al. 2002).

The trends were weaker in the three studies on the central the northern mainland of BC. One explanation for the more variable data is that these studies involved only a single year of surveys and sampled each station for 1-3 days, although in the Vancouver Island and Olympic studies significant trends emerged after the first season of surveys. Another likely explanation is that the very large watersheds opening into the long fjords of the mainland coast are used by relatively few murrelets. It is also possible that the habitat associations of Marbled Murrelets on the central and northern mainland differ from those on western Vancouver Island. Finally, the effects of variable prey availability at sea have not been investigated and in some areas this might limit local populations rather than areas of suitable nesting habitat.

4.5.4 Estimated densities of Marbled Murrelets from radar counts

Evidence for significant relationships between murrelet numbers and areas of suitable nesting habitat from the radar studies reviewed above suggests that densities derived from these studies (birds per ha of habitat) will be useful as a management tool. A density measure could be used to

calculate the area of forest needed for a specific population of murrelets, or conversely to estimate the numbers of murrelets likely to be using a specific area of forest. Densities from 108 watersheds from five radar studies in BC have been calculated using three different measures of suitable habitat in Appendix 3. In summary, this analysis indicates that densities on the west of Vancouver Island (Clayoquot Sound and northwest Vancouver Island) were almost identical and were significantly higher than those from the BC Mainland (Sunshine Coast, Central Coast and North Coast). Densities in the three mainland areas did not differ significantly.

The major problems in deriving and applying densities are in correctly defining and measuring suitable habitat. Several different measures of habitat had to be used in Appendix 3 because there was no common measure in all studies. This could be corrected by re-analysing the data using one or more measures applied to all the watersheds uniformly. As stressed in Appendix 3, the application of these interim density estimates in management decisions should be done with caution. For example, densities derived from general measures of habitat (e.g., all mature and old growth at all elevations) cannot be applied to selected patches of habitat known to contain a high proportion of likely nesting habitat. Ideally the habitat criteria used to derive the density measures should be the same as those used to apply them.

4.6 Mapping habitat features and the use of habitat algorithms

An important research goal for Marbled Murrelet conservation is to identify large-scale habitat parameters that are good indicators of nesting habitat and which can be used to map and measure such habitat. Most of the key features needed for nesting murrelets (accessible broad platforms, mossy substrates etc.) are not included in any of the usual Geographic Information System (GIS) criteria used for mapping forests. Some surrogate measures or algorithms (quantitative combinations) of several measures are needed for large-scale mapping and management. Several approaches have been taken to deal with this issue.

4.6.1 Sources of mapped habitat data

Satellite imagery – Raphael et al. (1995, in press) used a combination of Landsat imagery and regular forest cover data in GIS databases to map the distribution of habitat in western Washington, and test habitat associations using audio-visual data. Later, in their radar study, Raphael et al. (2002) commented that habitat classification from satellite imagery was not ideal, because many features that distinguish nest sites from non-nest sites could not be detected. Satellite imagery coupled with other habitat measures was also a key element in the large-scale analyses of murrelet habitat use in California and Oregon (Meyer 1999, Meyer and Miller 2002, Miller et al. 2002). In a pilot study covering Carmanah Valley, Landsat and KFA-1000 (Russian) data were combined with TRIM topographic data to develop an algorithm which was significantly correlated with several habitat features important for Marbled Murrelets (Jaques 1996). This proved the potential value of using satellite imagery for large-scale mapping, but this algorithm has not been applied or tested.

Forest cover maps – Timber supply cruising has provided estimates of tree size, stand age, timber volume (cubic metres of wood per ha) and other measures which can be assessed as indicators of suitable murrelet habitat. The scale used is usually 1:20,000.

Biogeoclimatic Ecosystem Classification (BEC) mapping – This system uses broad biogeoclimatic measures to classify and map forests in a standardized manner across BC (RIC 1998a). The smallest units (site series) are defined by regional climate, soil and ecosystem features (Green and Klinka 1994). Mapping usually involves biogeoclimatic subzones and variants which cover large tracts of similar elevation, climate and exposure. BEC classification (to the subzone level) is done at many scales but 1:500,000 up to 1:250,000 is appropriate. For smaller units (i.e., larger-scale mapping) site-series are sometimes mapped. BEC has been successfully used in developing algorithms for classifying and mapping suitable murrelet habitat (next section), and is most useful for analysis of large areas.

Broad ecosystem mapping - This is a mapping of very general (i.e., broad) ecosystem types, within biogeoclimatic and ecoregion units. Within the context of managing Identified Wildlife (Anon. 1999), a broad ecosystem unit is defined as a permanent area of the landscape, meaningful to animal use, that supports a distinct kind of dominant vegetative cover, or distinct non-vegetated cover (such as lakes or rock-outcrops). A broad ecosystem unit includes potential (climax) vegetation and any successional stages. Broad ecosystem units are meant to be used for small scale mapping of large areas, mainly at the 1:250,000 scale.

Terrestrial Ecosystem mapping (TEM) – Terrestrial ecosystem mapping is the mapping of ecosystem units that are a combination of site series (from BEC) and present structural stage of development. The site series are often split into various subdivisions as well, based on slope, aspect and soil/terrain features. As site series are units within BEC, the ecosystem units are nested within the biogeoclimatic classification and the ecoregion classification. TEM maps contain a biogeoclimatic classification of each polygon based on nutrient and moisture regime and the potentially resulting assemblages of vegetation (Green and Klinka 1994, RIC 1998b). TEM mapping is usually done at 1:20,000 scale, and sometimes up to scales of 1:5000.

Vegetation Resources Inventory (VRI) – VRI is forest cover mapping, based on air photo interpretation and topographic mapping, with some additional attributes to better describe vegetation physiognomy, cover and canopy structure (RIC 1997). It is not ecosystem mapping, although it can be used to generate an ecosystem map when combined with biogeoclimatic mapping and an interpretative algorithm taking into account species, soil moisture regime, and other attributes. VRI data are useful for murrelet studies because they focus on the tree layer and contain information on dominant tree species, average tree size, age, and structural measurements such as vertical canopy complexity. The scale used is usually 1:20,000.

Sensitive ecosystem inventory – SEI mapping done by the Conservation Data Centre (Wildlife Branch) and Canadian Wildlife Service was used by Burger et al. (2000b) on southeast Vancouver Island as a first step in identifying potentially suitable habitat polygons. They found that the SEI maps, which identify forest >100 years old, did not necessarily capture other

attributes of murrelet habitat. Only 30% of polygons identified by the SEI database were considered to be potentially suitable Marbled Murrelet habitat.

4.6.2 Algorithms for habitat mapping and selection of protected areas

Numerous algorithms and habitat models have now been developed to identify Marbled Murrelet nesting habitat in BC and elsewhere. Tripp (2001) reviewed 11 algorithms and models used in BC. She found that they fell into three broad categories:

- those developed to characterise and map the capability (potential for suitable habitat) and suitability (existing suitable habitat) of habitat based on structural stages and vegetation types in ecosystems (e.g., Demarchi 2001);
- those developed to apply the guidelines for Marbled Murrelets in the Identified Wildlife Management Strategy (IWMS; Anon. 1999), with the goal of identifying suitable habitat for Wildlife Habitat Areas (WHAs) and other protected areas in harvested areas (e.g., Manley and Jones 2000, Harper et al. 2001c);
- those developed using detailed modelling, often from original field research, which result in habitat suitability indices (HSI), often expressed as mathematical formula, and often providing some weighting to the more important variables (e.g., Bahn and Newsom 2002a, McLennan et al. 2000).

The spatial scales of the models, algorithms and habitat suitability maps range from the entire province (Demarchi 2001, Demarchi and Button 2001a,b), through large regions (Manley and Jones 2000, McLennan et al. 2000), down to specific management units, such as tree farm licences managed by a single company (Kremsater et al. 1999, Harper et al. 2001c). A sample of these is reviewed here, focusing on studies which have involved extensive field work to develop and test the models. Tripp (2001) provides a more detailed review. The analysis of nest sites in Desolation Sound has also involved the development of habitat models at stand-level (Waterhouse et al. 2002) and landscape-level (Huettmann et al., in prep.), which are reviewed in sections 4.3.1 and 4.5.1, respectively.

Vancouver Island - Chatwin (1999) developed the first landscape-level assessment for identifying suitable habitat for WHAs and other purposes on Vancouver Island. She applied the criteria in the IWMS requirements for Marbled Murrelets (Anon. 1999), such as distance from the sea and forest cover attributes, plus some additional data on nest requirements (platform height etc.) in a seven-step process. Key elements of this process were ground and aerial evaluations and audio-visual surveys to confirm the suitability of habitat that was selected by mapping the suitability criteria. This method is being assessed and applied in the selection of potential WHAs in several parts of Vancouver Island (e.g., Lindsay et al. 2000).

Following multi-year field studies in the Ursus Valley, Clayoquot Sound, Bahn (1998) developed a Habitat Suitability Index (HSI) model, based on procedures developed by the U.S. Fish and Wildlife Service (1980, 1981), which have been widely applied in North America (Gray *et al.* 1996). The HSI model produces quantitative indices using variables known or perceived to be important to a species. In his model, Bahn (1998) selected:

- Mean epiphyte cover on trees (EPIMEAN);
- Number of trees per ha with more than three platforms (DENTRPL4);
- Standard deviation of tree height (m) (SDHT);
- Canopy closure (CANCLVEG);
- Distance to the Ocean (km) (DISSEA);
- Altitude (m) (ALTITUDE);
- Distance to the nearest forest edge (m) (DISEDGE).

For each variable, a graph was produced which portrayed the relationship between the variable and some measure of suitability (in this case the log-transformed index of the ratio of occupied to visual detections, LNIRACO). One example of such a graph is shown here, along with the suitability index derived from it (Figure 4.9).

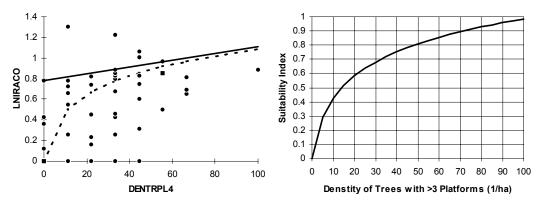


Figure 4.9: Construction of the suitability index for the number of trees per ha with >3 platforms (DENTRPL4) in Marbled Murrelet breeding habitat. Left, the scatterplot with DENTRPL4 ratings of 51 stations in the Ursus Valley against the mean occupied detection rate (LNIRACO). The solid line is the least absolute deviation 90th quantile regression line and the dotted line is the logarithmic description of habitat suitability. Right, the translation of the fitted logarithmic function (suitability index = 0.265 * LN(0.02 * DENTRPL4 + 0.05) + 0.795) in a suitability index from 0 to 1. From Bahn (1998).

Finally, the various indices were combined into a single predictive equation:

$$\mathbf{HSI} = \left[\left(\frac{CANCLVEG + SDHT + 2*EPIMEAN + DISEDGE}{5} \right)^{\frac{1}{4}} * (DENTRPLA4)^{2}*DISSEA*ALTITUDE \right]^{\frac{1}{8}}$$

Bahn (1998) intended this exercise to show how various parameters important to murrelets might be combined into a single algorithm. Several of these criteria would not be available on large-scale GIS databases, but the HSI could be developed using mappable parameters.

This approach was expanded by Bahn and Newsom (2002 a) in developing a HSI model which could be applied to Vegetation Resource Inventory (VRI) maps for all of Clayoquot Sound, and the output of the evaluation model displayed as GIS maps. These maps could be overlaid with maps evaluating other criteria, such as recreational areas, scenic corridors, and riparian areas for land management purposes. They used VRI maps because Terrestrial Ecosystem Map (TEM) polygons had not provided strong correlations with Marbled Murrelet activity in previous studies (Bahn et al. 1999) and because their own results indicated that VRI maps were more appropriate.

The VRI polygons were first stratified according to the mean height of the dominant tree species (TOPHT):

- Low (0-25 m TOPHT);
- Medium (26-35 m TOPHT);
- High (>35 m TOPHT).

HSI models were then produced, in a similar manner to Bahn (1998) using the following variables from VRI and Terrestrial Resource Inventory (TRIM) topographic maps:

- height of dominant trees (TOPHT), corrected for elevation;
- age (years) of the leading tree species;
- basal area (m²/ha) of canopy and emergent trees;
- vertical canopy complexity (four classes: 1-4, based on the height differences between the highest and the lowest trees in the polygon);
- canopy closure (%) of the tree crowns;
- average distance of the polygon from the ocean;
- average elevation of the polygon (m above sea level).

The application of this habitat suitability model to 338,499 ha of land area on 1:20 000 map sheets in Clayoquot Sound resulted in this classification:

- 34,833 ha (10.4% of the total area) of important-excellent habitat
- 40,466 ha (12.1% of the total area) of important-good habitat
- 59,388 ha (17.7% of the total area) of sub-optimal habitat
- 200,440 ha (59.8% of the total area) of unsuitable habitat.

In order to test the validity of some of the mapping criteria, Bahn and Newsom (2002b) compared audio-visual detections at 11 paired stations selected using VRI maps in Clayoquot Sound. Each pair consisted of one station in a Low TOPH category (trees <26 m tall) and one in a High TOPH category (trees >35 m), which were sampled on the same morning. As predicted, the highly ranked habitat had significantly higher rates of occupied and subcanopy detections than the low ranking habitat, but there were no differences in total detections (which include a high proportion of birds nesting elsewhere) (Table 4.13).

Table 4.13. Comparison of Marbled Murrelet activity and physical characteristics in 11 paired stands tall and short trees, sampled on the same morning. Means are given ± SD. From Bahn and Newsom (2002b).

Activity Measures	Short stands (tree height <26m)	Tall stands (tree height >35m)	Statistical test results	<i>P</i> -value
Total detections	20.6 ± 16.9	20.7 ± 12.1	t = 0.04	0.970
Occupied detections	0.27 ±0.55	2.39 ± 2.30	t = 3.39	0.007
Subcanopy detections	0.02 ± 0.08	0.77 ± 1.01	t = 2.60	0.026

Data from habitat plots done by Conroy et al. (2002) generally confirmed the applicability of the Bahn and Newsom (2002 a) model. Trees in habitat rated as Excellent had thicker epiphyte growth, were taller, and had greater diameter at breast height than trees in Good or Sub-optimal habitats. Tree density was lower and canopy closure was higher in Excellent habitat than in Good

and Sub-optimal habitats. Good and Excellent habitats had higher densities of platforms and higher densities of trees with platforms than Sub-optimal habitat. The distribution of nests located by telemetry in Clayoquot Sound (F. Cooke, unpubl.) will provide another means of assessing the validity of the Bahn and Newsom (2002 a) model. The habitat model developed by Waterhouse et al. (2002) from analysis of nest sites at Desolation Sound resulted in parameters and predictions that were remarkably similar to those in the Bahn and Newsom model (see section 4.6.2).

Elsewhere on Vancouver Island Harper et al. (2001c) provide an example of a model developed to identify and map suitable habitat as defined by the 1999 IWMS criteria (Anon. 1999). This was done to assist the company (Canadian Forest Products, Ltd.) to identify areas suitable for WHAs within their licence area in the Nimpkish Valley. The model was developed in conjunction with field work to identify the relationships between mappable parameters and nest habitat parameters, such as availability of potential platforms (Harper et al. 2001a,b). Briefly, they developed a 5-class system of grading habitat potential (very high, high, moderate, low, and nil), which involved ranking forest polygons in a hierarchical 4-step process. The first step was a coarse filter to eliminate stands that were too young to provide nesting platforms, and ranked stands based on age classes. Steps 2 and 3 involved applying a similar ranking process successively using tree height and site productivity, respectively. The final step was to use Biogeoclimatic Ecosystem Classification (BEC) to identify and down-rate high-elevation subzones unlikely to provide platforms (e.g., MHmmp), allowing management to focus on more likely nesting habitat.

In the same study, Harper et al. (2001a) compared densities of potential nest platforms per ha in non-contributing landbase (including Provincial Park, ungulate winter range and steep inoperable terrain) with land included in the timber harvesting landbase. Platform densities were significantly higher in non-contributing forest (mean 415 platforms per ha) than in timber harvesting landbase (228 per ha). These differences were largely due to differences in elevation of the two categories, and when elevation was controlled by stratifying the data by biogeoclimatic subzone, there were no significant differences. In the CWHvm1 zone, where most plots occurred, platform densities averaged 234, 178, and 234 per ha in ungulate winter range (35 plots), steep inoperable (19 plots), and timber harvesting landbase (33 plots), respectively (no variances reported).

Queen Charlotte Islands/Haida Gwaii - Following a review of relevant information, Burger (1999) identified mappable parameters likely to be useful on these islands, and developed ranking criteria for each parameter. Collectively these criteria provided an algorithm which could be applied to forest cover and other maps at both the landscape (1:250,000) and stand (1:20,000) scales. McLennan et al. (2000) tested these algorithms by applying them to Broad Ecosystem Inventory GIS database, and also Terrestrial Ecosystem Mapping (TEM) databases in some areas. They tested the validity of the selection with field transects, and then refined the algorithm criteria to give better accuracy in predicting and rating forest polygons. The McLennan et al. (2000) algorithms have been widely used and modified in BC and so are described in some detail here.

The density of potential nest platforms (limbs >18 cm in diameter with no apparent height restriction) was used as the main measure of habitat quality by McLennan et al. (2000). Four categories were used:

- low (platform density 0-50 per ha);
- medium (51-150 per ha);
- high (151-300 per ha);
- very high (>300 per ha).

These categories were then used as field measures of murrelet habitat quality to compare with habitat ranking based on the algorithm applied to forest cover map data.

Following initial tests and revisions, the final algorithm based on the forest cover data used:

- forest age class (with maximum weighting of 20 given to age class 9 (251+ years);
- height class (with maximum weighting of 20 given to class 7 and 8 (>55.5 m);
- canopy closure (maximum weighting 10 to classes 4,5 and 6 intermediate canopy closure from 36-65%);
- elevation (maximum weighting 10 for 0-300m, and 7 for 300-600 m etc.);
- slope (maximum weighting 5 for slopes <35%)

Tree species showed no association with measures of platform density and could not be used in the mapping algorithm.

The procedure was to score each polygon for each of these measures, and then add the scores, giving a maximum of 65 points for each polygon. Polygons were rated as:

- no value (total score <19);
- poor or unsuitable (19-46);
- fair or potentially suitable (47-55);
- good or suitable (56-60); and
- superior or highly suitable (>60)

The ability of the revised algorithm to correctly identify the correct category of habitat based on the density of potential platform limbs (per ha) was tested. The revised algorithm correctly identified 46% of the 76 transects using forest cover mapping data, and 61% using habitat actually measured in the transects. In most cases the mis-classification was either by one rating class or one class of platform density. The algorithm tended to over-classify relative to the map data and underclassify relative to the field data.

McLennan et al. (2000) also developed a separate algorithm for Tree Farm Licence 39 that had no forest cover mapping. Here they used biogeoclimatic site-series categories and TEM mapping. Within each of four subzone variants (wh1, CWHwh2, CWHvh2 and MHwh), they ranked the site-series, based on platform densities measured in transects, and the RIC (1999) wildlife habitat ratings. The latter measure was also used to group the site series into 2-4 groups per subzone variant to simplify the model. They found a general trend of increasing platform density with increasing site productivity. From these data they developed a preliminary algorithm for Tree Farm Licence (TFL) 39 which used:

• age class, height class, elevation, and slope (as used in the algorithm for forest cover); plus

• site series grouping (four levels with high weighting, maximum 35 points). This algorithm has not been field tested.

In ground-truthing the GIS data, McLennan et al. (2000) found good agreement between the forest cover map data and field transect measures of some variables (leading species 70% match; age class about 75% match) but height class was less well matched (about 40%) and canopy closure had a very low match (<20%). In 70% of the transects, the field estimates of canopy closure were lower than the forest cover values based on aerial photographs. The forest cover maps systematically overestimate canopy closure. This was given a low weighting in the final algorithm.

McLennan et al. (2000) also discussed the need for *capability* mapping which considers the potential for polygons to develop suitable murrelet habitat in the future (presumably after logging or other disturbance). This differs from *suitability* mapping, which considers the present age and integrity of the polygon.

The revised McLennan et al. (2000) algorithm was tested using a small sample of seven nest sites located by telemetry in 2000 (Manley et al. 2001). When applied using mapped criteria the algorithm was less successful than when applied with habitat data from transects on the ground. The nest sites were in forest classified as Unsuitable (4 sites), Potentially Suitable (1), and Suitable (2) based on mapped data, but the numbers of sites in each class were 2, 1 and 4, respectively, based on transect data. All the sites fell within the Medium (5 sites) or High (2 sites) platform density classes of McLennan et al. (2000). A larger sample of nests is needed to adequately test the algorithm.

An interesting extension of the McLennan et al. (2000) algorithm was used in negotiations over the placement of WHAs in the Eden Landscape Unit to meet the IWMS (Anon. 2001). The constraints imposed on including land in the Timber Harvesting Land Base (THLB) meant that most of the protected areas would have to fall within forest classified as Non-contributing Land Base (NCLB). The range of error in classifying forests, especially in the "potentially suitable" habitat, had been documented in the McLennan et al. (2000) study. In the Eden landscape most of the NCLB was either ranked potentially suitable or unsuitable. Most of the suitable habitat fell within the THLB. To avoid including forest within WHAs that was mapped as potentially suitable, but in reality might have been unsuitable, an attempt was made to calculate the number of potential platforms needed to meet the IWMS requirements. Numbers of potential nest platforms, rather than area of potentially suitable habitat was proposed as the unit of negotiation. Forest patches which had fewer potential platforms (and were thus assumed to be less likely to support many murrelets) were therefore discounted, and areas with higher platform densities were given greater weighting. It remains to be seen whether this is an acceptable and reliable method of selecting Marbled Murrelet habitat. Ideally some confirmation of platform densities, using either a helicopter or ground surveys, or evidence of occupancy by murrelets, should be mandatory for all WHAs and other protected areas proposed for murrelets.

Sunshine Coast – Manley and Jones (2000) applied the criteria for selecting WHAs stated in the IWMS requirements (Anon. 1999) in a model to identify and map all potential WHAs in the Sunshine Coast Forest District. Polygons were ranked as potential WHAs on the basis of:

- size (minimum 200 ha as recommended by the IWMS, although some smaller polygons were included where necessary);
- stand age (selected polygons were to be largely, but not necessarily entirely, composed of 250+ year-old forest);
- stand height (selected polygons were to be largely, but not necessarily entirely, composed of trees = 19.5 m tall, i.e. height class 3, which is less than recommended by the IWMS);
- edge (efforts were made to minimise the amount of forest edge in selected polygons).

WHAs were delineated by GIS using MOF and forest company forest cover maps.

The selected polygons were then assessed using the following criteria to rank habitat quality:

- the proportion of the polygon in age class 9 (>250 years old);
- size (area of the potential WHA with larger ones ranked higher);
- percent of the polygon in High and Medium quality class (a simple ranking scheme was used which combined height class and biogeoclimatic BEC variants, which were selected as proxies for changes in platform density with increasing elevation).

Within the Sunshine Coast Forest District 25% of all Landscape Units had less than 12% (the upper limit of the 10-12% IWMS goal; Anon. 1999) of the forest area within age class 9 stands. When stand size and configuration were considered 58% of all Landscape Units had less than 10% of potentially suitable habitat. In other words, there simply was not enough remaining old-growth to meet the IWMS requirements. Manley and Jones (2000) went on to discuss five management options, given the limited availability of suitable habitat. Jones (2000) made other recommendations, including raising the management of Marbled Murrelets in the Sunshine Coast Forest District to Higher Level Planning and the development of a biologically relevant target for protected areas.

One goal of the Sunshine Coast study was to assess the proportion of potential WHAs in operable vs. inoperable forest, and the suitability of these two forest categories as murrelet nesting habitat. The Ministry of Water, Land and Air Protection and the Ministry of Forests have directed that WHAs for Marbled Murrelets should be placed in inoperable (non-contributing) forest where possible. Jones and Manley (2001) report that:

- inoperable stands had significantly lower frequencies of total, visual and occupied detections of murrelets;
- data from plots showed that inoperable stands were on much steeper slopes (as expected) but there were no significant differences in forest gap area, density of trees with platforms, and density of platforms;
- data from transects showed that inoperable stands had significantly lower density of trees with platforms, fewer platforms per ha, and higher mistletoe indices, but no significant differences in mean diameter or height of trees, or moss and lichen cover on branches.

The data indicate that WHAs situated entirely in non-contributing forest on the Sunshine Coast were likely to provide suboptimal habitat which appeared to be used by fewer murrelets.

4.6.3 Province-wide mapping of the distribution and change of habitat

The first attempt to quantify and map Marbled Murrelet habitat across the entire province was made by Demarchi and Button (2001a,b). Habitat ratings were based on the standard six-class system for wildlife in BC (RIC 1999), and were developed by Demarchi (2001) in collaboration with government wildlife biologists familiar with murrelets. These were then applied to habitat polygons derived from 1:250,000 Broad Ecosystem Inventory mapping. This scale allows only a coarse analysis of habitat availability and is not suitable for management at landscape or watershed levels. This analysis is still being refined, and the results summarised here might change with improved habitat ratings. It is best to treat the following results as hypotheses, requiring further testing. The existence of apparently suitable habitat does not necessarily indicate use by nesting murrelets; other factors such as availability of suitable foraging areas are also important.

Two maps were produced by this process. The first shows habitat **capability** (Demarchi and Button 2001a), indicating the likely pre-industrial distribution of suitable inland habitat in the past, based on biogeoclimatic conditions. The map shows an almost continuous distribution of habitat capability ranked moderate, high or very high through most of the BC coast, with the exception of eastern Vancouver Island, the northeastern portion of Graham Island (Queen Charlotte Lowlands) and several of the large islands along the Central and Northern Mainland coasts.

The second map shows habitat **suitability** (Demarchi and Button 2001b) indicating the likely distribution and ranking of inland nesting habitat at the present time. Comparisons between the capability mapping (predicted historical) and suitability mapping (present status) show considerable changes in many areas, mainly due to industrial logging, urbanization and agriculture (Figure 4.10). Demarchi (2001) stressed that comparisons of habitat suitability and capability provide a meaningful expression of the loss of habitat potential but do not provide a measure of absolute habitat loss (i.e., square km lost).

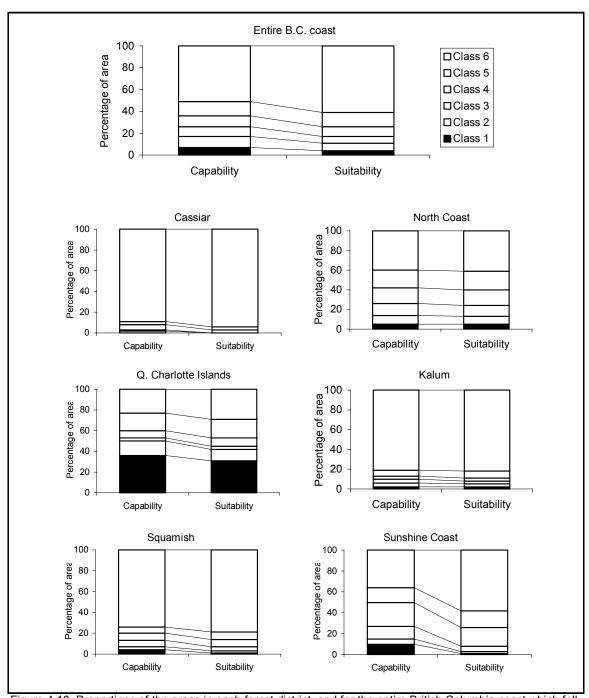


Figure 4.10. Proportions of the areas in each forest district, and for the entire British Columbia coast which fell into the six habitat categories for Marbled Murrelets (Demarchi and Button 2001a,b). The differences between habitat capability (based on biogeoclimatic characteristics) and habitat suitability (present conditions), reflect the changes which have occurred in each forest district. The habitat categories were: 1: Very High; 2: High; 3: Moderate; 4: Low; 5: Very Low; 6: Nil (RIC 1999). Continued on the next page.

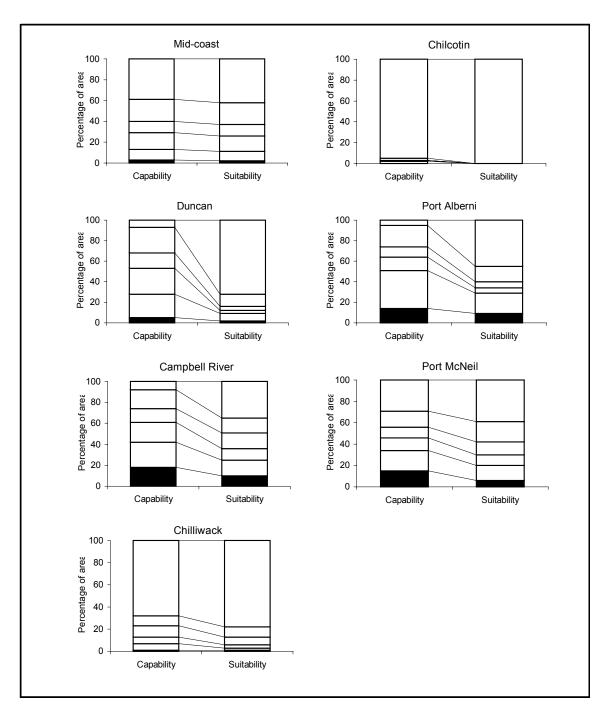


Figure 4.10 (continued).

Data on the availability of currently suitable habitat are valuable in determining the relative abundance and distribution of murrelets, the degree of flexibility available in land management, and the relative importance of each forest district in maintaining a large provincial population of murrelets. The differences between capability and suitability are valuable in indicating districts where there have likely been significant reductions in murrelet populations. Collectively these data also help identify districts in which special efforts are needed to maintain viable populations in order to preserve the geographic range of the species in BC.

Taking classes 1-3 (moderate, high, and very high nesting capability or suitability) as indicators of the most likely habitat to support nesting murrelets, we can make a preliminary assessment of the availability and changes in this habitat in each forest district (Table 4.14).

Table 4.14. Likely changes in the availability of moderate to very high quality nesting habitat (habitat classes 1-3 combined) for Marbled Murrelets in each forest district, and for the entire B.C. coast (data from Demarchi and Button 2001a,b). Capability represents the ability of the land base to produce habitat in which murrelets could nest, and suitability represents the current availability of such habitat. In this table the combined % area within the top 3 habitat classes is shown, along with the % change from capability to suitability. Forest districts are ranked from highest to lowest % capability. This analysis is still being refined and these data may change as habitat ratings improve.

	Percentage of the a		
Forest district	Capability	Suitability	% change
Port Alberni	64	34	46.9
Campbell River	61	36	41.0
Q Charlotte Islands	53	45	15.1
Duncan	53	12	77.4
Port McNeil	46	30	34.8
Mid-Coast	29	26	10.3
Sunshine Coast	27	8	70.4
North Coast	26	24	7.7
Squamish	13	7	46.2
Chilliwack	13	6	53.8
Kalum	10	8	20.0
Cassiar	3	0	100.0
Chilcotin	3	0	100.0
Whole BC Coast	26	17	34.6

Although derived from fairly general and incomplete habitat models, these data are useful in at least two ways. First, they can be used to identify areas where attention is needed to maintain the geographic distribution of the species in BC and prevent further decline in severely reduced but geographically important populations. The preliminary data suggest that special efforts are needed in the Sunshine Coast, Squamish and Chilliwack forest districts to maintain the

geographic distribution. Parts of the Campbell River, Port Alberni and Duncan districts on the east of Vancouver Island fall into this same category. Cassiar and Chilcotin districts appear to have lost all their moderate or better habitat, but had very little to begin with (at the heads of long inlets or fjords), and probably contributed little to the provincial population size or distribution.

Second, the mapping data are useful for identifying areas where attention is needed in order to maintain a large provincial population. Forest districts which had high habitat capability but which have apparently lost a considerable portion of that habitat include: Port Alberni (47% reduction); Campbell River (41% reduction); Duncan (77% reduction); Port McNeil (35% reduction); and the Sunshine Coast (70% reduction). Other districts which still have a high proportion of moderate or better habitat in which there has been relatively little reduction include the Queen Charlotte Islands (15% reduction), Mid-Coast (10% reduction) and North Coast (8% reduction).

A useful addition to the mapping exercise would be to identify the areas and proportion of each habitat suitability class presently within protected areas in each forest district. This would allow a better overview of the conservation needs within each district. Ideally this should be done at a finer scale than for forest districts, because many districts include several widely different biogeoclimatic zones and areas with different logging histories (e.g. eastern and western Vancouver Island in the Duncan, Port Alberni and Campbell River districts).

Some of the capable habitat has been permanently changed. The Fraser Valley lowlands and delta once supported extensive forests with nesting capability for murrelets, but virtually none of this remains, and there is little chance of it ever being restored. For this reason Demarchi and Button (2001a,b) did not include this area in their mapping. Likewise most of eastern Vancouver Island from Sooke through Campbell River has lost capable forests to cities, towns, agriculture, roads and other permanent developments. Much of the remaining forest land in this area is privately owned, and subjected to logging cycles which are unlikely to produce old-growth conditions suitable for murrelets.

4.7 Fragmentation and edge effects in forest habitat

4.7.1 Background

Understanding the responses of Marbled Murrelet to fragmentation of their nesting habitat is critical to evaluate the impacts of logging on present and future populations, and for planning meaningful habitat reserves for the species. Forest fragmentation is the process of subdividing contiguous forest into smaller pieces, and is an inevitable consequence of clearcut logging. Fragmentation has several interlinked results: reduction of available habitat, changes in the spatial patterns of this habitat, and increases in forest edges. All of these are likely to affect Marbled Murrelets and it is often difficult to identify the critical changes effecting murrelets and the mechanisms of the impacts (Marzluff and Restani 1999, Marzluff et al. 2000, Raphael et al. in press).

Raphael et al. (in press) summarised potential effects of forest fragmentation on Marbled Murrelets, which makes a useful starting point for this review (Table 4.15). All of the changes associated with fragmentation are likely to have negative impacts on murrelets (- symbol) or to be neutral (0 symbol). The only likely positive impact, not considered by Raphael et al. (in press), is access to nests by flying murrelets, which is likely to be improved by fragmentation, but is probably offset by increased predation risk.

Table 4.15. Potential short term and long term* effects of fragmentation of nesting habitat on local population size and demographics of the Marbled Murrelet in the Pacific Northwest (from Raphael et al. in press).

Fragmentation effect on nesting habitat	Population size	Adult survival	Number of nests	Nest success
Reduced amount of nesting habitat	0/-	0/0	0/-	-/0
Smaller patch size (reduced area of interior habitat, increased edge)	0/-	0/0	-/-	-/- **
Increased number of patches***	0/0	0/0	0/0	0/0
Increased isolation of patches	-/-	-/-	0/-	-/0

NOTES

Raphael et al. (in press) suggested that reduced amount of nesting habitat was likely to have long-term negative impacts on the number of nests and short-term impacts on nest success which would both ultimately reduce population size (Table 4.15). The short-term consequences of loss of habitat are still poorly known, but murrelets are thought to exhibit site fidelity within landscape units (Nelson 1997) and if so, birds returning to newly logged areas might not breed for several years until established elsewhere. Radar counts in Clayoquot Sound (Burger 2001) suggest that when old-growth habitat was reduced murrelets did not pack into the remaining habitat in higher densities, and watershed numbers declined. The lag-time between loss of habitat and change in local population is not known.

Smaller patch size, associated with increased edge effects and reduced interior core area, is likely to have negative short-term effects on the number of nests (especially if murrelets are reluctant to nest in higher densities in remnant forest patches) and on nest success (due to edge effects). The strength of the edge effects will depend on the suite of nest predators found locally, because the various predators respond differently to edges and forest fragmentation (discussed in more detail below). These changes will ultimately reduce populations in the long term. The effects of smaller

^{*}Symbols to left of slash are short term effects (<10 years), symbols after the slash are longer term effects (>10 yr, but generally several decades). Symbols are: - (negative or deleterious); 0 (neutral); + (positive). A negative effect on any demographic parameter is assumed to cause population decline in the longer term.

^{**} Effects will vary depending on the suite of predators at the particular sites. This might depend on the agent of fragmentation and resulting habitat matrix. Some predators are more abundant in continuous forest, others respond to edge.

^{***} Effects given for number of patches per se, all else relatively equal (but in the larger context of fragmentation we assume these patches would be smaller, in addition to being more numerous).

patches on adult survival are not known, nor are the responses to patch size of predators likely to take adult murrelets, such as falcons (Raphael et al., in press). Increased patch number *per se* is not likely to have any impacts, but decreasing patch size is a necessary consequence of increasing patch number, so the effects of patch number can probably never be tested.

Increased isolation of patches might have negative short-term impacts by increasing the risks of predation to adults flying to isolated patches across less hospitable clearcuts or immature forest (Raphael et al. in press). This in turn is likely to impact nest success and ultimately number of nests and the total population size. In California and southern Oregon, potentially suitable forest patches more than 5 km from other active nesting areas were less likely to be occupied by murrelets than those less than 5 km apart, and no occupied plots were more than 11 km from other sites with occupancy or presence of murrelets (Meyer 1999, Miller et al. 2002).

Marzluff and Restani (1999) and Raphael et al. (in press), identified *potential* impacts of forest fragmentation on Marbled Murrelets, but few studies have clearly identified the actual consequences of fragmentation (Manley 1999, Manley and Nelson 1999), or the causes of negative impacts (Marzluff et al. 2000). Known consequences of forest fragmentation are first reviewed below, followed by a review of climatic and predation factors which are known or likely to have impacts on murrelets.

4.7.2 Placement of nests relative to edges

Many nests have been found at or near forest edges (Figure 4.11). In a sample of 30 nests from the Pacific Northwest, the mean distance to edge was 92 ± 131 m (range 15-700 m; Hamer and Nelson 1995). There might have been a bias in these data, because nests near edges might be more readily found by ground-based observers.

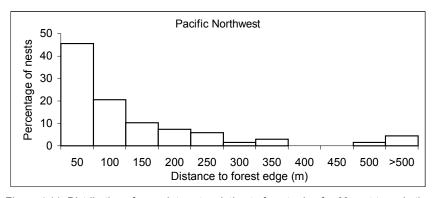


Figure 4.11. Distribution of murrelet nests relative to forest edge for 68 nest trees in the Pacific Northwest (Hamer and Nelson 1995).

Few studies of Marbled Murrelet nest locations have differentiated between natural edges (created by forest clearings, boulder fields, creeks and blowdowns) and man-made edges bordering roads, recent and regenerating clearcuts. Preliminary analysis of nests located by radio-telemetry in Desolation Sound (R. Bradley 2002 and unpublished data) indicates that murrelets

often nest within 10-20 m of natural edges, but the sample is insufficient to determine whether the same applies to man-made edges (Figure 4.12).

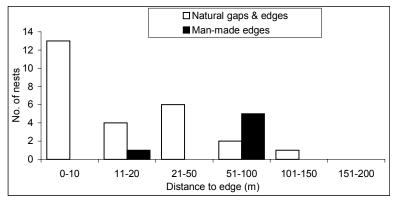


Figure 4.12. Distance to natural gaps and edges (canopy gaps, creeks, boulder-fields etc.) and mad-made edges (clearcuts, roads, immature forest) from Marbled Murrelet nests found by radio-telemetry in Desolation Sound, B.C. (R. Bradley, unpubl. data).

In all data on distance to edge there was no information on the proportions of available forest area relative to the forest edge, which is necessary to test whether the murrelets were specifically selecting nests in proximity to an edge, or whether this distribution simply reflects the availability of habitat. Most data come primarily from areas where there has been considerable fragmentation of forests (most of Hamer and Nelson's 1995 data came from Washington and Oregon), where much of the suitable forest might be in small stands close to edges. Some of the stands in both samples were small enough that the nests could not be >200 m from an edge in any direction.

Relatively few nests have been found in the less fragmented forests of southwest Vancouver Island. Seven nests found after seeing murrelets land or selected because they seemed likely nest trees (Selected) were all within 100 m of the forest edge or a stream, whereas nests found in randomly selected trees (Random) were less likely to be near the forest edge or stream (Figure 4.13).

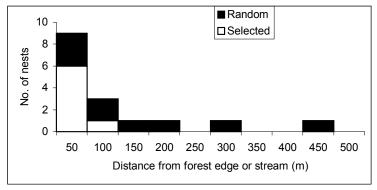


Figure 4.13. Distribution of nests relative to forest edge or nearest stream on southwest Vancouver Island (data from A. Burger, unpubl.; Conroy et al. 2002; Jordan et al. 1997). Selected trees were those climbed after seeing murrelets land or because they seemed likely nest trees, random trees were those randomly selected in tree-climbing plots.

Overall, murrelets did not necessarily nest in proximity to forest edges, but in fragmented habitats many nests were found within 100 m of a forest edge. To a murrelet approaching a nest, the possible benefits of flying over open ground, such as a road, clearcut or immature forest, would not extend beyond 50 m into an old-growth stand (and more likely <20 m), so it seems unlikely that this is the only explanation for a high proportion of nests found within 100 m of forest edge in highly fragmented stands. It seems more likely that this reflects the availability of suitable forest in such stands, but this remains to be tested.

4.7.3 Nest success relative to proximity to edge and patch size

Nelson and Hamer (1995) found that successful nests were significantly further from forest edges (mean 155.4 m) than nests which failed (mean 27.4 m), and all successful nests, except one, were >55 m from the forest edge. This trend persisted when the sample was enlarged to include more recent data from across the Pacific Northwest (Manley and Nelson 1999, unpubl. data; see also Raphael et al. in press). For 58 nests with known locations (from Oregon and BC; I. Manley and K. Nelson, unpubl. data), the success of nests within 50 m of a forest edge was 38% (n = 29) and for those >50 m from an edge was 55% (n = 29), but this difference is not statistically significant ($\Box^2 = 4.55$, P>0.05). Successful nests were significantly further from edges (mean 141 m) than failed nests (mean 56 m). Predation was responsible for the failure of 60% of all active nests in these samples, and predation rates were higher within 50 m of edges than further into the forest interior. All 13 nests that were >150 m from an edge were successful or failed from reasons other than predation. There was a trend for successful nests from Oregon and BC to occur in larger stands (mean 491 ha) than unsuccessful nests (mean 281 ha), although this was not statistically significant (P = 0.12).

Bradley (2002) analysed the success of nests found by telemetry in Desolation Sound, relative to their proximity to forest edges. He conducted two analyses. One was from ground-based measures of distance from edge and nest success from 37 accessible nest sites, analysed at 50 m and 100 m scales. At both spatial scales, there was no significant differences in nest success at sites adjacent to or far from forest edges. Most nests were located adjacent to natural edges rather than artificial ones. Comparing nest success at natural and artificial edges was difficult, because only two nests were located directly adjacent to artificial edges (both were successful). The second analysis was a coarse-scale GIS analysis using 98 nest sites, looking at edge type within 200 m of sites based on 1:250,000 landscape classification maps. In this analysis the proportions of sites adjacent to edges vs. interior were similar to those in the first ground-based sample. As in the first analysis, many nest sites were adjacent to natural edges, predominantly avalanche chutes, and the majority of these nesting attempts was successful (79%, n = 42). Nest success near artificial edges (61%, n = 23) and in forest interior (48%, n = 33) was lower. Nests adjacent to natural edges had significantly higher success than those in the forest interior (P = 0.007), but there were no significant differences between nests adjacent to artificial vs. natural edges and artificial edges vs. interior forest (P>0.05). In summary, Bradley's (2002) analysis did not support the hypothesis that nesting near forest edges was harmful to murrelets, but could not resolve whether natural or artificial edges produced differences in nest success.

The difficulties in locating active nests and tracking their success has precluded detailed studies of the causes of nest failure relative to patch size and distance from edges. To overcome these limitations, Marzluff and his collaborators have used simulated nests (discussed in section 4.7.7).

4.7.4 Causal factors in fragmentation: microclimatic changes

Contiguous old-growth forests have microclimatic regimes which differ sharply from those of clearcuts or young regenerating forests. In general, extremes of temperature and solar radiation are minimized, and humidity in summer is higher and more stable in old-growth forests than recent clearcuts (Chen et al. 1999). Changes in microclimates can have both direct and indirect effects on nesting murrelets. Direct effects include thermal stress (both hot or cold) and dehydration if adults or chicks are exposed to direct sunlight or increased winds. Indirect effects are most likely to occur through changes to the availability of moss pads and other epiphyte growth on which most murrelet nests have been found.

There are sparse data on the tolerance of murrelet adults and chicks to radiation and thermal stress. A downy murrelet chick placed in late afternoon sun in California began panting within a minute and moved into nearby shade (Binford et al. 1975), indicating that such chicks are sensitive to solar radiation. On the other hand, this same chick had evidently tolerated several hours of hot direct sunlight to which its nest site was exposed on typical summer days, suggesting that such stress could be tolerated. Nelson and Wilson (1999) documented the death of a nestling from renal failure, which appeared to be a consequence of dehydration as a result of being provisioned by only one parent.

Likewise there are very few data on the effects of microclimate and exposure to edges on the nesting microhabitat of murrelets. At exposed coasts on the Queen Charlotte Islands, Rodway et al. (1991) found fewer murrelets and fewer mossy platforms than farther inland, which they attributed to salt spray inhibiting moss growth. Burger et al. (2000a) found significantly fewer of the microhabitat canopy features important to murrelets for nesting at coastal stations up to 250 m inland: fewer potential nest platforms, fewer trees with platforms, thinner epiphyte mats on the boughs of large trees, and less structural diversity in the canopy. Severe winter storms and year-round salt spray apparently inhibited epiphyte growth, blew off thick moss mats, pruned off dead limbs likely to provide platforms, and created a more uniform canopy surface. Foliage above nest platforms, which reduces exposure to weather and predators, appeared less common over platform limbs at the coast than in the interior, but was not quantified.

It is important to consider the distance that microclimatic effects penetrate from edges into the remaining forest where murrelets are likely to nest. Based on a review, but with relatively little data from the Pacific Northwest, Kremsater and Bunnell (1999) suggested that microclimatic effects associated with forest edges extend up to 2 to 3 tree heights (i.e., 100-150 m) into the forest in this region. The most detailed work in the region was that of Chen et al. (1993, 1995, 1999) in old-growth Douglas-fir in Washington, which showed that changes in microclimate extended from clearcut edges well into interior forest. Factors likely to effect murrelets or their nest habitat, such as increased air temperature, solar radiation and wind speed typically extended 30-60 m into the forest, but were strongly influenced by edge orientation, and temperature and

wind effects could extend beyond 240 m into the forest. It is not known whether such changes might negatively impact nesting murrelets. The increase in air temperatures due to edge exposure on clear sunny days averaged 3.6 °C (max. 7.0 °C) higher than interior forest. This increase seems unlikely to be sufficient to trigger heat stress in a murrelet, but this does not take into account solar radiation absorbed. Increased solar radiation in Washington Douglas-fir forest typically extended 15-60 m from the edge, depending on orientation (Chen et al. 1995).

Natural edges, such as riparian edges along streams, also create microclimatic gradients, but these appear less severe than at clearcut edges (Chen et al. 1999). In Douglas-fir forests in western Washington, for example, temperature and humidity gradients along stream edges extended 30-60 m into the forest, but solar radiation and wind speed gradients were not detectable (Brosofske et al. 1997).

The unknown question is whether any of these deviations in microclimate associated with forest edges, although statistically significant, would have significant effects on nesting murrelets (such as increased insolation causing over-heating, or cold wet winds causing cold stress, might cause adults to abandon incubation if thermally stressed) or the microhabitat that they typically nest in (such as causing moss to blow off platform limbs). Microclimatic effects will change with elevation, aspect and surrounding topography as well, making it difficult to apply general rules to designing WHAs and other protected areas.

4.7.5 Causal factors in fragmentation: predation

Predation consistently emerges as the most significant cause of nest failure in Marbled Murrelets, and is also an important cause of adult mortality (see section 2.7). The distribution and abundance of some predators are strongly affected by forest fragmentation and proximity to forest edges, which consequently affects the murrelets. There is, however, no consensus on the effects of fragmentation and edge on avian nest predation and relatively few studies have been done within the range of the Marbled Murrelet. The entire suite of predators needs to be considered (Marzluff and Restani 1999). Increased predation due to edge-loving species (e.g., some corvids) might have minimal impact if there is more intense predation by predators not affected by edges (e.g., some mice), or predators that prefer forest interior (e.g., some squirrels). In Marzluff and Restani's (1999) review, studies which showed no significant edge effects typically had diverse predator assemblages of birds and mammals, whereas studies showing significant edge effects had often considered only part of the predator community. They also suggested that fragmentation and edges might not necessarily cause any additional impacts in situations where nest predation rates were high.

Given the diverse community of potential nest predators in western North America, Marzluff and Restani (1999) predicted that forest edges bordering on regenerating forest would be unlikely to exhibit strong edge effects, but there have been too few studies to confirm this prediction. Proximity to human activities, which promote populations of crows and ravens, and the presence in clearcuts of berry-producing plants, which attract jays, were likely to be significant factors affecting nest predation in western forests.

In their review of recent literature from across the world, Marzluff and Restani (1999) found that edge effects were more common in forest fragments within urban or agricultural matrices than in forest fragments surrounded by regenerating forest (which is usually the situation for Marbled Murrelets in logged areas). In this last category, Marzluff and Restani (1999) found significantly increased nest predation associated with forest edges in only 21% of 19 studies, but there were significant effects in 57% of the 7 studies which considered the effects of forest fragment size.

4.7.6 Distribution of predators relative to fragmentation and edge

In Clayoquot Sound, Rodway and Regehr (2002) compared the frequencies of occurrence of potential predators during 2 h dawn survey periods among edge and forest stations, and in fragmented and unfragmented forest stands (Table 4.16). Potential murrelet predators were more abundant at ocean edge than interior stations, which may reduce the attractiveness of coastal areas to nesting murrelets. Steller's Jays (P < 0.001) and Northwestern Crows (P < 0.001) were reported during a greater percentage of surveys in fragmented than unfragmented forest. Occurrence of Common Ravens (P = 0.387) and Bald Eagles (P = 0.71) did not differ between fragmented and unfragmented areas. Red squirrels were reported during a greater proportion of surveys in areas that were unlogged than in partially logged areas (P = 0.035).

Table 4.16. Comparison of the percentage of surveys during which potential Marbled Murrelet predators were recorded at ocean edge, on stream channel, and at forest station locations, and in partially logged and unlogged areas of Clayoquot Sound in 1997 (Rodway and Regehr 2002).

	Number of surveys	Steller's Jay	Common Raven	Northwestern Crow	Bald Eagle	Red Squirrel
Location						_
Ocean edge	29	21	14	66	48	17
Stream channel	188	11	5	9	14	12
Forest	150	7	3	2	3	13
Logging						
Fragmented	42	26	2	29	14	2
Unfragmented	326	8	6	8	12	14

In a three-year study at 26 stations in Carmanah and Walbran valleys on Vancouver Island, potential predators were recorded during the standard two-hour dawn surveys for murrelets (Burger et al. 1997a). Steller's Jays were most common and were regularly reported from 24 stations regardless of their distance from the ocean (0.1-17.7 km inland). Common Ravens were similarly distributed, but less common than jays. Northwestern Crows and Bald Eagles were common at coastal stations, but rare inland (see also Burger et al. 2000a). Stations were classified as being disturbed (on roads or in recent clearcuts logged <10 years before) or undisturbed (>100 m from roads or clearcuts), and the frequency of human use, predominantly camping, picnicking or hiking, was classified as high (people likely to be encountered several times a week) or low (people likely at intervals of more than a week). At inland stations, the % occurrence and densities of Steller's Jays and all predators combined were significantly higher at disturbed than undisturbed stations (Table 4.17; Mann-Whitney test, P<0.01 in each case). The densities of Common Ravens were significantly higher at disturbed than undisturbed stations (P<0.05), but

the % occurrence showed no significant difference (P>0.05). Percentage occurrence and densities of owls and red squirrels did not differ between disturbed and undisturbed stations (P>0.05 in each case). The effects of human use were tested separately within disturbed and undisturbed stations (Table 4.17). The only significant difference found was within disturbed stations, where the % occurrence and densities of Steller's Jays were higher with high human use than with low use (in both tests P<0.05).

Table 4.17. Mean (± SD) percentage occurrence of predators per survey and density (number of predators per survey) at 26 stations in the Carmanah and Walbran watersheds in 1994-1996 (Burger et al. 1997b).

	Mean percentage occurrence per survey				Mean no. predators per survey			
	All	Steller's	Common	Red	All	All	Steller's	Common
Station classification	owls	Jay	Raven	Squirrel	predators	owls	Jay	Raven
Disturbed inland stations *								
High human use (4 stations)	16 ± 15	91 ± 9	31 ± 28	18 ± 32	94 ± 7	0.2 ± 0.1	1.9 ± 0.4	0.7 ± 0.4
Low human use (3 stations)	35 ± 31	64 ± 4	17 ± 17	22 ± 19	83 ± 17	0.5 ± 0.5	0.9 ± 0.2	0.2 ± 0.2
All disturbed stations	24 ± 23	79 ± 16	25 ± 23	20 ± 26	89 ± 13	0.3 ± 0.3	1.4 ± 0.6	0.5 ± 0.4
Undisturbed inland stations**								
High human use (7 stations)	2 ± 3	43 ± 24	13 ± 12	20 ± 11	63 ± 23	0.02±0.03	0.6 ± 0.5	0.2 ± 0.1
Low human use (10 stations))28 ± 31	37 ± 33	7 ± 16	42 ± 37	63 ± 30	0.4 ± 0.5	0.5 ± 0.4	0.1 ± 0.2
All undisturbed stations	17 ± 27	39 ± 29	9 ± 14	33 ± 31	63 ± 27	0.2 ± 0.4	0.5 ± 0.4	0.1 ± 0.1

^{*} station on road or in a clearcut logged within past 10 years

The same study also compared the relative density of Steller's Jays at observation sites used to measure potential prey for goshawks on southwestern Vancouver Island. There was a significant difference between the mean density of jays at sites with >5% logging disturbance within 200 m $(0.35 \pm 0.81 \text{ [SD]})$ jays per station, N = 43) than at undisturbed stations $(0.16 \pm 0.46 \text{ [SD]})$ jays per station, N = 172 stations; t = 2.04, P<0.05). Jays were recorded at 21% of disturbed sites and 13% of undisturbed sites.

The type of forest edge is often important in determining the occurrence of predators. Two studies on southwest Vancouver Island found that densities of Steller's Jay were higher at artificial forest edges (roads and clearcuts) than at natural edges. Point counts made in three valleys found significantly higher counts at road and clearcut edges than at river edges or interior forest (Figure 4.14; Kruskal-Wallace test, P = 0.002).

^{**} station >100 m from roads or clearcuts

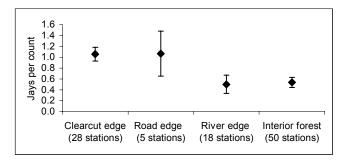


Figure 4.14. Relative densities (birds per count) of Steller's Jay measured in point counts made in the Klanawa. Carmanah, and Walbran valleys, southwestern Vancouver Island (A. E. Burger unpubl. data). Three 10-min counts, separated by >14 days were made at each station between 15 May and 15 August 2000. Means ± SE shown.

In a two-year study of Steller's Jay, Masselink (2001) found a significant difference in jay density between river, road and clearcut locations (Figure 4.15). Counts were not quite significantly different (P = 0.07) when testing the additional effects of core vs. edge habitats, although the differences were large for clearcut and road edges.

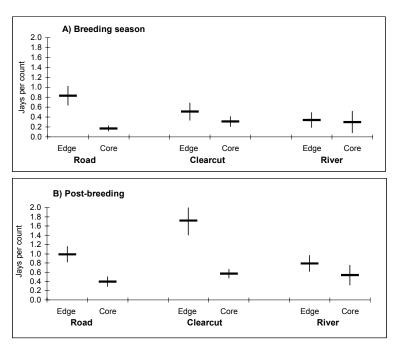


Figure 4.15. Mean number of jays (± SE) detected per 10-minute point count at forest edge and forest core stations for each location type investigated during breeding (A: 1997 data only; 3 surveys per station) and post-breeding (B: 1996 and 1997 data combined; 6 surveys per station). Data from Carmanah and Walbran valleys, Vancouver Island (Masselink 2001).

Using radio-telemetry, which overcomes some of the potential bias associated with visual and auditory surveys, Masselink (2001) also recorded the spatial distribution of Steller's Jays relative to the forest edge. Jays were divided into those caught in clearcuts and those caught in the forest interior. The distribution of these groups differed, but jays in both groups were most frequently found within 50 m on either side of the forest-clearcut boundary (Figure 4.16). Masselink (2001) also quantified the vertical distribution of the jays to determine their likely exposure to canopy-

nesting murrelets. Overall, the 11 jays were found in the forest canopy on 26% of the telemetry re-locations, indicating a relatively high risk to murrelets nesting within 50 m of the forest edge.

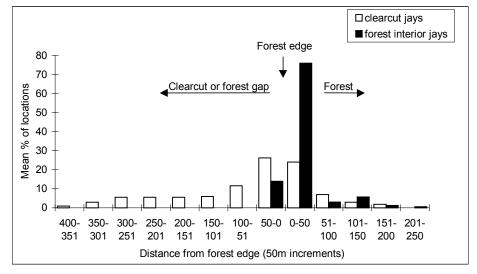


Figure 4.16. Distribution of radio-tagged Steller's Jay relative to forest edge. Birds were divided into two groups: those caught in the clearcut (n = 6), and those caught in the forest interior (n = 5). Each jay was located at random times, for an average of 28 times (range 8-47 locations). Note that direct comparison between clearcut and edge jays cannot be made, because the forest interior jays did not have access to clearcuts, only roads or rivers, and hence could not cover the full range of distance categories accessible to the clearcut jays. From Masselink (2001).

In a study of the effects of patch size on birds in the Nimpkish Valley on Vancouver Island, the most common predators were the corvids: Gray Jay, Steller's Jay, Northwestern Crow and Common Raven (Schieck et al. 1995). In all four species measures of relative abundance and percentage occurrence increased with forest fragmentation (i.e., there was a negative correlation with patch size), although none of the trends was statistically significant.

A five-year study in Washington and Oregon, found that corvids, particularly Steller's Jays, were common along forest edges that bordered early-seral vegetation with berry-producing bushes (Marzluff et al. 1999, 2000, Luginbuhl et al. 2001, Raphael et al. in press). Corvids, especially crows and ravens, were usually most common close to human activities, including towns, roadways, campgrounds, picnic areas, and refuse dumps. In southeast Alaska, densities of Steller's Jay were higher at edges bordering clearcuts and wetlands than in the interior forest, while those of red squirrels were higher at wetland edges but not near clearcut edges (De Santo and Willson 2001). In coast redwood forests in California, Steller's Jay was found to have highest relative densities within 50 m of abrupt forest edges (both natural and man-made; Brand and George 2001). Relative densities gradually declined within the forest to level off at about half the edge density beyond 150 m.

Northern Goshawks frequently forage along forest edges (Squires and Reynolds 1997), but telemetry studies in southeast Alaska showed that they did not use edges more frequently than forest interior, relative to the availability of these habitats (Iverson et al. 1996). Female goshawks were found within 300 m of beaches more often than expected, but males did not show this pattern.

4.7.7 Predation risk relative to fragmentation and edge

There have been few detailed studies of edge effects and nest predation in the types of habitat used by Marbled Murrelet for nesting in the Pacific Northwest. Bryant (1994) reported significantly more rapid predation of artificial nests less than 100 m from forest edges in montane habitat on Vancouver Island, and suggested that Steller's Jays might have been a cause of this pattern. De Santo and Willson (2001) found that predation of artificial nests was higher in areas with higher predator densities in southeast Alaska. Higher nest predation was reported from forest edges bordering suburbs, where Steller's Jays and Northwestern Crows were common, and along clearcut edges, openings and interior forest where red squirrels and jays were common. In both of these studies the artificial nests were low in the trees relative to where murrelets nest, but jays (Masselink's 2001) and squirrels (Carey 1995,1996) spend a considerable portion of their foraging time in higher canopies, in addition to foraging close to the ground.

The most intensive research on the likely impacts of forest structure and landscape contiguity on Marbled Murrelet nest predation has been done by Marzluff and associates in the Olympic Peninsula, Washington, and in Oregon (Marzluff et al. 1999, 2000, Luginbuhl et al. 2001, Raphael et al. in press). They used painted plastic eggs and stuffed, dark-coloured chicken chicks to simulate the eggs and chicks of Marbled Murrelets, and placed these on high limbs (in likely sites for murrelet nests) in a range of different habitats, but primarily in Douglas-fir forests. Many precautions were taken to reduce human scent and other factors which limit the use of artificial nests in predation studies. The disturbance and removal of these eggs and chicks was monitored by motion-sensitive radio-transmitters within the decoys and the type of predator was identified from beak and tooth marks on wax coatings around the eggs and wax inside the mounted chicks. Video cameras monitoring other simulated nests and experiments with captive mammals confirmed the abilities and likelihood of various predators to attack eggs and chicks. The simulated nest trials were designed to test the effects of three factors:

- *stand structure*, classified as: simple mature (80-120 years old, canopy single-storeyed with few gaps]; complex mature [80-120 years old, canopy 1-2 storied with many gaps]; and very complex old-growth [>200 years old, multi-storied canopy with many gaps]);
- *proximity to humans*, classified as near (<1 km) and far (>5 km) from towns, farms, campgrounds, dumps, highways, etc.);
- *landscape contiguity*, classified as fragmented (plot >75% surrounded by clear-cuts) or contiguous (plot >75% surrounded by mature forest).

Survival of simulated nests varied relatively little among the various habitat types, and there were no consistent effects of forest fragmentation on nest survival (Figure 4.17). The highest nest survival occurred in mature forest with simple structure which were either contiguous and near human activity or fragmented and far from humans. The lowest survival occurred in mature, simple forests near human activities, and in old growth within 1 km of human activity, where fragmentation was unimportant. Densities of corvids were lowest in contiguous, simple structured maturing forests, regardless of proximity to humans, and corvid numbers differed little among the other habitat categories. It is difficult to infer generalizations from these results, but Marzluff et al. (2000) suggested that old-growth stands used by murrelets for nesting might be

best buffered by surrounding the stands with maturing, simple-structured forests in which there were relatively few predators.

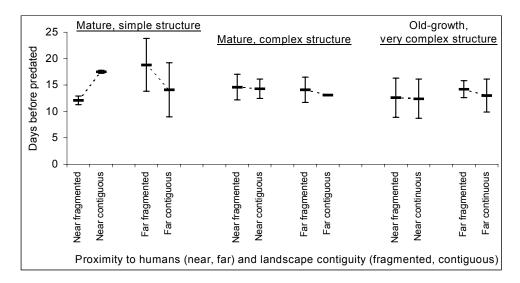


Figure 4.17. Effects of forest structure, proximity to humans, and landscape contiguity on the index of survival (mean number of days before predated) of simulated nests of Marbled Murrelets on the Olympic Peninsula, Washington (data from Marzluff et al. 2000).

In the same study, Luginbuhl et al. (2001) reported a strong negative correlation between survival of simulated murrelet eggs and corvid abundance at the landscape level (5-50 km² scale). Corvid abundance explained 69% of the variance in predation of simulated murrelet eggs. This trend was not evident at smaller plot-level scales (0.5-1.0 km²). The cause of this scale-sensitive relationship was likely due to the large home range of some of the corvid species (ravens and crows), and the consequences of this for monitoring and management purposes are that such negative correlations might not be evident unless large spatial scales are considered.

The reduction and fragmentation of old-growth forests can also lead to the undesirable situation in which murrelets and some of their predators (especially old-growth dependent species such as goshawks) are restricted to using the same small patches. This could lead to greater risk of predation. If adult murrelets are put at risk in this way it would have serious consequences for populations.

4.7.8 Summary of fragmentation and edge effects on murrelets

The three processes linked with forest fragmentation which Raphael et al. (in press) identified as likely to have negative impacts on murrelets (Table 4.15) can now re re-assessed. The effects of reductions in habitat remain rather ambiguous, with considerable anecdotal evidence for long-term reductions in regional populations where there has been extensive logging, but virtually no hard data on the extent or mechanisms of these reductions (Ralph et al. 1995b). The close correlation between murrelet counts made with radar and existing old-growth areas in several independent studies suggests that murrelet numbers are strongly dependent on the areas of suitable forest available, and decline as habitat is reduced (see section 4.5.3). The short-term

effects of reduced habitat in delaying or preventing some adults from breeding have not been studied.

The edge effects associated with smaller patches and fragmentation have received more attention, particularly possible changes in predation risk, but effects of changes in microclimate remain unknown. The two analyses of nest success relative to edges showed somewhat conflicting results: the review of nests from across the Pacific Northwest found evidence of negative effects of edge (Manley and Nelson 1999, Raphael et al. in press), whereas the analysis of nests from the telemetry study in Desolation Sound showed no negative effects of artificial forest edges, and higher success at natural edges than in interior forest (Bradley 2002; see Section 4.7.3). Likewise, some studies in the Pacific Northwest using artificial nests found negative effects from edges and fragmentation, whereas the more detailed study by Marzluff and associates found no simple relationships, and proximity to humans and stand structure seemed more important than edge and fragmentation (Marzluff et al. 1999, 2000, Luginbuhl et al. 2001, Raphael et al. in press).

Predation is the major cause of nest failure, and corvids are often responsible. Steller's Jay was the most numerous corvid in most areas where murrelets have been studied, although crows are more common along ocean shores and near human activities. There is strong evidence from several studies reviewed above that Steller's Jays are most common at or near forest edges, especially those bordering clearcuts and roads. Jays are most likely to be found within 50 m of forest edges, and since they spend substantial amounts of time in the forest canopy, they pose a significant risk to murrelets which might nest along such edges. Crows and ravens were sometimes, but not always found in association with forest edges. All corvids, but crows in particular, were strongly attracted to human activities. Corvid populations have been increasing in the Pacific Northwest (Marzluff et al. 1994), including BC (Campbell et al. 1997) and seem likely to continue to increase with increasing human populations, settlements, fragmentation of the forests and creation of new clearcuts which support berry-producing plants.

The greatest uncertainty with regard to fragmentation effects lies with the distribution, abundance and impacts of predators other than corvids. Raptors and owls capable of taking murrelets are relatively uncommon. Many species show no obvious associations with edges or fragmented forests, but there are insufficient data to conclude that this predation risk can be ignored. Similarly the information on the distribution and risks of predation from mammals is sparse and inconclusive. Experiments with captive squirrels and mice show that they are certainly capable of killing murrelet chicks, and remote monitoring showed that these mammals frequently visited simulated murrelet nests, but there are no confirmed cases of murrelet chicks or adults being killed by mammals. The studies reviewed above of flying squirrels, Douglas squirrels and chipmunks on the Olympic Peninsula, and red squirrels on Vancouver Island, suggest that these mammals are not strongly associated with forest edges, fragmented forests or human activities, and are often associated with interior forests. Similar results have been found with squirrels in other forest types (Pierre at al. 2001). More research is needed in the forests used by Marbled Murrelets, to complement the work done in Washington and Oregon by Marzluff and his co-workers

4.7.9 Management implications and optimal patch size

One of the key questions in the application of the BC Forest Practices Code for Marbled Murrelet conservation is the optimal size and shape of protected areas. The guidelines for Marbled Murrelets within the Identified Wildlife Management Strategy (IWMS) of the Forest Practices Code call for the creation of Wildlife Habitat Areas (WHAs) which should be a minimum of 200 ha, but may be smaller where 200 ha of suitable habitat is not available (Anon. 1999). Larger WHAs are preferred in order to provide interior forest conditions. WHAs should be a minimum of 600 m in width. If WHAs are <200 ha or minimal width is <500 m, buffers 100 m wide of oldgrowth or advanced second growth (>60 years) should be included around the nesting habitat.

The application of the IWMS has been restricted by additional requirements that wherever possible WHAs for murrelets should be incorporated into areas set aside for biodiversity, and in addition should be placed in forest that does not contribute to timber harvests (see Introduction). In practice it has proved difficult in some areas to find suitable habitat that meets these criteria and which is also in stands >200 ha, and this is hindering the creation of WHAs for murrelets. There are therefore suggestions that the 200 ha stand guidelines be relaxed and smaller areas set aside as protected nesting habitat for murrelets.

This issue is addressed here in two ways: first by considering the likely edge effects in smaller stands using a simple geometric analysis, and second by modelling nest success using the results of the geometric analysis applied to known edge effects on murrelet nests.

Geometric estimates of edge effects with varying size of stand - This section presents some simple calculations which estimate the extent of edge effects with varying size of forest stand and with varying penetration of the edge effects. Laurance and Yensen (1991) consider this topic in more detail.

Nearly all stands being considered as protected areas for Marbled Murrelets have complex boundaries and topography, which require GIS programs to model edge effects. Laurance and Yensen (1991) produced a model which predicts edge effects based on the shape index (a function of the perimeter length and total area) which is also applicable to more complex shapes. One can demonstrate some of the trends likely to occur using simple geometric shapes. This exercise used a circle, a square and two rectangles, one with sides in the ratio of 1:4 and the other 1:8. A circle, having the smallest boundary length per unit of area of any shape, gives the minimum edge effects. A square gives the minimum edge for a shape with right angles. The rectangles approximate the shapes of stands along riparian corridors.

From simple geometry, formulae giving the proportion of edge-effected area relative to the total area (P_e) were derived, using d as the symbol for the distance from the perimeter that edge effects penetrate in each case.

For a circle: $P_e = d(2r - d)/r^2$

where r is the radius of the circular stand.

For a square: $P_e = (4dL - 4d^2)/L^2$ where L is the length of one side of the square.

For a rectangle with side dimensions in the ratio 1:4: $P_e = (10dL - 4d^2)/4L^2$ or with sides in the ratio of 1:8: $P_e = (9dL - 2d^2)/4L^2$ where L is the length of the shorter side of the rectangle.

These equations were used to model the effects of edge in stands from 10 to 1000 ha, assuming that edge distance (d) was either to 50 m or to 100 m. The former seems the most likely effect from corvids attracted to edges, such as Steller's Jays (reviewed above), but there is a possibility that both weather and predator effects might extend to 100 m from edges (Kremsater and Bunnell 1999). Along ocean edges on SW Vancouver Island, for example, both the habitat changes and increased predator densities extended at least 250 m into the forest (Burger et al. 2000a). The results from these models illustrate several important points relevant to Marbled Murrelets (Figure 4.18). In particular the effects of reducing stand size from 200 ha to smaller sizes can be examined. The effects discussed here assume that patches are surrounded on all sides by unfavourable habitat; if old-growth patches were bordered in part by older second growth buffering the edge effects, the affected portion of the patch would, of course, be less. All of the shapes considered here underestimate the effects of edge likely in complex "amoeba-shaped" polygons which have high edge: area ratios.

First, edge effects obviously cover a greater portion of the stand if they penetrate to 100 m than to 50 m. For 200 ha stands, effects penetrating to 50 m include 12-22% of stands, depending on the shape, whereas those penetrating to 100 m include 23-43%. This result highlights the need for accurate estimates of the penetration of edge effects.

Second, the predicted changes are non-linear and increase in an exponential manner as stand size declines below 200 ha. For example, decreasing stand size from 200 to 100 ha causes an increase in the proportion of edge-affected area by 37-40% (slight variations according to the shape and penetration distance), whereas decreasing stand size from 200 to 50 ha causes an increase in edge-affected area of 87-95%, i.e. edge effects almost double. For very large stands the changes due to stand size become almost linear, but since there is no clear point of inflexion it is impossible to designate an optimal stand size (Laurance and Yensen 1999).

Finally, the shape of the stand has a significant effect on the affected area. Edge effects are least in circular or square stands but increase rapidly as the stand becomes more elongated (Figure 4.18). For example, with 200 ha stands and 50 m penetration, the edge effects cover 12%, 14%, 17% and 22% of the stand area with circles, squares, 1:4 rectangles and 1:8 rectangles respectively. Elongated or amoeboid polygons with more complex boundaries will have still higher proportions affected (Laurance and Yensen 1999).

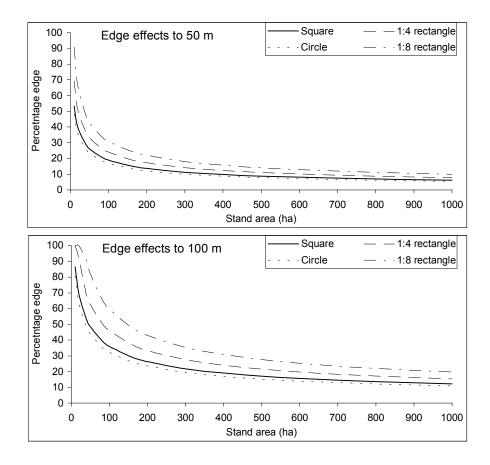


Figure 4.18. Percentage of the stand affected by edge effects which penetrate to 50 m (upper graph) and 100 m (lower graph) in circular, square, and rectangular (with side ratios 1:4 and 1:8) stands.

The effects of splitting a protected area into multiple portions area also evident (Figure 4.19). In this example, a 200 ha protected area is either intact or split into 2-10 portions, and the edge effects penetrate to 50 m. The total protected area remains the same (200 ha), but the proportion affected by edge effects increases. The more complex the shape of the stands the more rapidly edge effects increase with fragmentation (i.e., steeper slope to the curves).

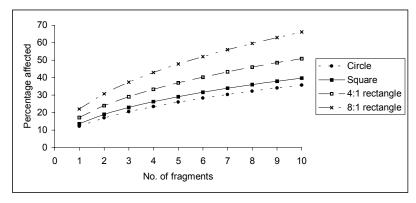


Figure 4.19. Percentage of the area affected by edge effects if a 200 ha protected area is split into 2-10 fragments, and the edge effects penetrate to 50 m.

Modelling nest success with stand size – Possible effects of fragment size on nest success in Marbled Murrelets can be modeled, using the results of the geometric analysis above and recent estimates of nest success relative to edge proximity. Across the Pacific Northwest 38% of nests within 50 m of forest edges were successful, compared to 55% of those >50 m from edges (Manley and Nelson 1999, unpublished data).

If these measures are applied to the proportions of the stand which fall into the outer 50 m or inner core, we can estimate the average nest success for the stand (Figure 4.20). This was done for only circular (the shape with the least edge) and 1:8 rectangular shapes (a more realistic shape for forest polygons). For stands larger than 200 ha the proportion in the 50 m edge perimeter is relatively low and overall nest success changes little with stand size. Below 200 ha, and particularly below 100 ha, the proportion of the stand in the edge zone increases and hence overall nest success for the stand declines. The effect is minimal for circular stands but more marked for the more realistic 1:8 rectangles, and would be even more striking for elongated or amoeboid forest polygons with a high perimeter:area ratio.

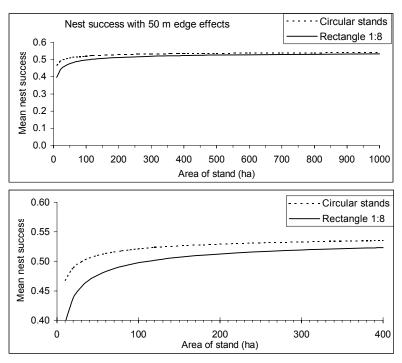


Figure 4.20. Effect of changing stand size on average nest success (proportion of nests which fledge chicks), based on the proportion of the stand within 50 m of the edge, and mean nest success of 0.38 within 50 m of an edge, and 0.55 for areas >50 m of an edge (Manley and Nelson 1999, unpubl. data). The lower graph shows the same data in greaterdetail for stands <400 ha. Circular plots represent the shape with the lowest edge effects and 1:8 rectangles represent more realistic stand shapes.

The changes in average nest success with declining stand size do not appear too severe, but a long-term and widespread reduction in nest success caused by forest fragmentation might be sufficient to tip the balance between a stable and a declining population (see sections 3.1.10 and

3.1.11). This model considered the most conservative penetration of edge effects likely in BC forests (50 m). Obviously if predation and microclimate associated with edges penetrated further the decline of nest success with declining forest stand would be more severe.

4.7.10 Conclusions on the effects of forest fragmentation

The effects of fragmentation and edge on nesting success of murrelets remain unclear. On balance it seems prudent to treat the creation of artificial, "hard" edges by clearcutting as a negative impact, because there is no evidence that murrelets benefit from such edges, and some evidence that these edges are detrimental. This is particularly likely in areas where corvids are common and likely to be the main nest predators. Reductions in old-growth forest might force Northern Goshawks and Marbled Murrelet into the same habitat patches, which would increase the risk of predation to murrelets. This is particularly concerning because goshawks kill adult murrelets which is likely to have a greater impact on local populations than loss of eggs or chicks.

There is much stronger evidence that fragmentation of old-growth forests is detrimental because of the absolute reduction in habitat, and radar studies show strong correlations between habitat area and murrelet populations. Some landscape-scale studies (Raphael et al. 1995, 2002, in press, Meyer 1999, Miller et al. 2002) indicate negative effects on murrelets of fragmentation and spatial isolation of suitable forest stands.

Many questions remain unanswered in considering the effects of fragmentation and forest edges on murrelets, including:

- microclimatic effects which might reduce moss cover and other nest-site attributes;
- the effects of the entire guild of predators on murrelets and their nest contents;
- the distribution of murrelet nests relative to natural and man-made edges, and in relation to the availability of edge and interior habitats;
- the roles of forest regeneration from clearcut to mature forest on edge effects.

Finally, it seems likely that total habitat area and habitat quality are more likely to have strong effects on populations of nesting Marbled Murrelets than patch size. This is emerging as a general trend from ecological modelling (Fahrig 1997, Fleishman et al. 2002). Patch size should not be ignored when managing nesting habitat for Marbled Murrelets, especially when patches are bordered by abrupt forest edges, but population size seems more likely to be affected by the total habitat area and quality of nesting habitat than by patch size.

4.8 Effects of elevation on Marbled Murrelets

4.8.1 Distribution of nests relative to elevation

Murrelet nests have been found from sea level to 1530 m elevation. In a sample of 35 nests from the Pacific Northwest, the mean elevation was 332 m (range 14-1097; Hamer and Nelson 1995),

but there might be a bias towards lower elevations if these sites were more accessible to people (Huettmann et al., in prep.). Nests found by telemetry avoid elevation bias (section 4.5.1), and provide data from Desolation Sound (83 nests; Huettmann et al., in prep.), Mussel Inlet (12 nests; Kaiser and Keddie 1999), Clayoquot Sound (17 nests; Wildlife Ecology Chair, SFU, unpublished) and Queen Charlotte Islands/Haida Gwaii (7 nests; Manley et al. 2001). These are plotted against elevation in Figure 4.21. Overall, 84% of the 119 nests were found below 1000 m, and there was a rapid drop-off in nests with increasing elevation above 1000 m. Outside Desolation Sound, 75% of the nests were below 600 m and all were below 900 m. Comparison of nest placement vs. distribution of forests in Desolation Sound indicates proportionately higher use of forests between 200-600 m (see section 4.5.1).

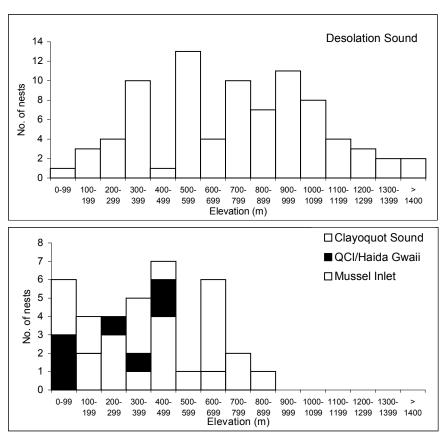


Figure 4.21. Distribution of nests found by radio-telemetry in BC relative to elevation. The larger sample from Desolation Sound (83 nests; Huettmann et al. in prep.) is plotted separately from nests found in Mussel Inlet (12 nests; Kaiser and Keddie 1999), Clayoquot Sound (17 nests; SFU Wildlife Ecology Chair, unpubl.), and Queen Charlotte Islands/Haida Gwaii (Manley et al. 2001).

4.8.2 Effects of elevation on predation risk

The effects of elevation on predation rates and risks of predation for nesting Marbled Murrelets have not been specifically investigated. There are also few data on the distributions and abundance of potential predators relative to elevation in BC. The following information provides some indications of elevational trends but this was not an exhaustive literature search, and there are too few data to reach firm conclusions. In most of the information reviewed below, elevation

is inferred from biogeoclimatic subzones, which differ in elevational range, but also have many structural and floristic differences (Green and Klinka 1994). It is thus impossible to separate the inter-related effects of elevation and habitat on the potential predators.

Raptors – Campbell et al. (1990) provide the following information for known or suspected murrelet predators:

- Bald Eagle found 0-2400 m, but primarily at low elevations on coast, rivers, and lakes;
- Sharp-shinned Hawk found 0-2590 m, nests 0-900 m, but known to breed at higher elevations;
- Cooper's Hawk prefers low elevations, usually below 1400 m, nests 0-1130 m;
- Northern Goshawks found 0-2290 m, nests 0-1400 m;
- Peregrine Falcon strongly coastal distribution.

Telemetry studies of Northern Goshawks in southeast Alaska found that females were more likely to remain at low elevations below 250 m, but males, which do most of the hunting while breeding, were found at all elevations in proportion to their availability (Iverson et al. 1996). There was, however, relatively little (13%) land above 600 m in this study. Goshawks hunted over all slopes available (up to 37 degrees), and showed a slight tendency to use steeper slopes more often than expected.

Owls – Campbell et al. (1990) provide the following information for known or suspected murrelet predators:

- Western Screech-owl nests all below 540 m, but might be biased by large nest-box sample;
- Great-horned Owl found 0-2040 m, but less common at higher elevations, nests 0-1220m;
- Northern Pygmy-owl found 0-1710 m, often in high elevations, nests 490-1220 m;
- Barred Owl found 0-1250 m, nests 90-1100 m.

In the Nimpkish Valley, northern Vancouver Island, Setterington (1998) analysed data from three years of call-playback surveys, and compared 40 ha plots which contained owls with randomly-selected plots. Elevation was not investigated as a parameter but there were significant differences in owl vs. random plots in the proportions of the four biogeoclimatic zones, which included CWHxm2 (approximate elevation range 0-400 m; Green and Klinka 1994), CWHvm1 (400-600 m), CWHvm2 (600-950 m), and MHmm1 (950-1200 m). Compared with random plots, plots containing Western Screech-owls, Barred Owls, Northern Pygmy-owls and Saw-whet Owls contained significantly higher proportions of low-elevation CWHxm2, and lower proportions of CWHvm2 and MHmm1, but there was no difference in the low-elevation CWHvm1. Greathorned Owls were too scarce to show trends. Overall, these data suggest that the owls were more likely to occur in the lower elevations below about 600 m.

Corvids – Campbell et al. (1997) provide the following:

- Gray Jay widespread but mainly from 400 m to timberline, common in subalpine forests;
- Steller's Jay found 0-1500 m on coast, prefers lower elevations than Gray Jay;
- Northwestern Crow found 0-1700 m, but most common at low elevations near the coast:
- Common Raven widespread, found 0-2200 m and often in high elevations, nests 0-600 m on coast.

Point-count data from the Nimpkish Valley (TFL 37) in northern-Vancouver Island were grouped by biogeoclimatic subzone, which correspond to increasing elevation, with some overlap between CWHxm2 and vm1 (Figure 4.22; J. Deal, unpublished data). Significant differences in counts were found among the subzones for all three species, and for combined totals of all corvids (ANOVA, P<0.05; J. Deal, unpublished). Overall, corvids were more common in the low and mid elevations and less common in the higher vm2 subzone.

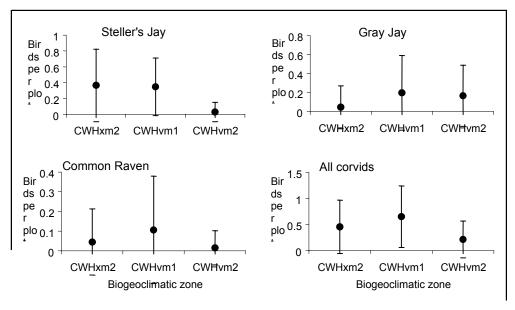


Figure 4.22. Mean ± SD counts per plot of corvids in three biogeoclimatic zones in TFL 37, mid- to northe Vancouver Island (J. Deal, unpublished data). The approximate zone boundaries were: CWHxm2: 0-400 CWHvm1: 0-600 m or 400-600 when xm present; CWHvm2: 400-950 m (Green and Klinka 1994). In this area the existence of plateaus sometimes blurs these boundaries (J. Deal, pers. comm.). Sample sizes were 67, 33 and 33 plots for xm2, vm1 and vm2, respectively; each plot was surveyed 3 tin

Waterhouse et al. (in prep.) compared counts of forest birds in low elevation Coastal Western Hemlock (CWH; generally below 1000 m; Green and Klinka 1994) and in high elevation Mountain Hemlock (MH; generally 1000-1600 m) zones in the Sunshine Coast and Southern Mainland. The index of abundance (least square means of individuals per 75 m radius point counts in 1992 and 1993) in CWH and MH was 0.09 and 0.02, respectively, for Steller's Jays, and 0.04 and 0.19, respectively, for Gray Jays. The combined counts of these jays were higher in the high elevation MH (mean 0.21) than in CWH (mean 0.14). Steller's Jay showed a significant negative correlation with elevation, and Gray Jay a positive correlation, but in both species the relationships were weak ($r^2 = 0.15$).

Mammals – Data on the relative densities of arboreal mustelids, squirrels and rodents likely to prey on murrelet eggs or chicks at different elevations were not readily available.

All predators - Bradley (2002) examined the relative index of predator abundance for Desolation Sound, determined from predator counts in 118 random habitat plots in twelve 100 m elevation classes. There was a significant decrease in predators (all predators, and all avian

predators) with increasing elevation (Figure 4.23). There was a strong outlier of high predator presence in the first elevation class (primarily coastal sites), but even after removing the outliers the negative trend was still significant. Examined alone, the Steller's Jay showed no such linear trend and was found in high numbers at around 700 m. There were no apparent elevational trends in the small mammal data (Bradley 2002).

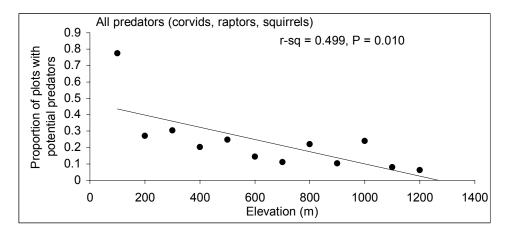


Figure 4.23. Change in the occurrence of potential predators of Marbled Murrelets with elevation in the Sunshine Coast, based on surveys at 118 randomly selected habitat plots (Bradley 2002). The proportions of plots with predators in each 100 m elevation interval with predators is shown, corrected for 1 hour of observation.

In summary, the available data suggest that most owls and raptors are usually more common in lower elevations (below about 900 m) than in higher areas. Distribution of corvids appears more complex, with no consistent elevational trends below about 1200 m for total corvid populations. There are insufficient data to conclude that predation risk for murrelets consistently changes with elevation, although higher numbers of predators are commonly found at or near the ocean shore. Marzluff and Restani (1999) caution that the entire suite of predators needs to be considered when assessing predation risk and this is not presently possible when assessing elevational effects. The distribution of arboreal mammals which might affect murrelets is particularly poorly known and difficult to measure.

4.8.3 Conclusions on the effects of elevation on nesting Marbled Murrelets

Knowledge of the distribution and success of Marbled Murrelet nests with increasing elevation is incomplete. The available data are sometimes contradictory, but some trends are evident. In BC murrelets are known to nest from sea level to about 1500 m in elevation, but the majority of nests fall below 1000 m. When nest distribution is compared with available habitat, some preference for low elevation nests (below 600 m) is evident (section 4.5.1).

The only data on nest success relative to elevation are from the nests found using telemetry in Desolation Sound (Huettmann et al., in prep.). These data indicate an increase in nest success

with increasing elevation, but the causes of this pattern are not known (see section 4.5.1). Bradley's (2002) analysis suggests that this might in part be due to early breeders, which are likely older more experienced birds, travelling further from foraging sites than late-breeding birds.

Predation appears to be the most common cause of nest failure, but there are no direct tests of predation rate at different elevations. Effects of elevation on predators, reviewed above, show no strong or obvious trends, and often contradictory evidence. It is premature to assume that predation risk consistently changes with elevation up to about 1000 or 1200 m.

Audio-visual surveys show declining detections of murrelets with increasing elevation. When analyses are focused on occupied or subcanopy detections, which eliminate long-distance detections and most commuting birds, this pattern is stronger (sections 4.3.2 and 4.5.2). Similarly, the distribution of stand-level and micro-habitat characteristics important for nesting (e.g., large trees, presence of potential platform limbs, epiphyte cover on branches) usually show significant negative associations with increasing elevation (section 4.4). The only exceptions to these trends come from areas where the low-elevation forests are greatly depleted, and the remaining low-elevation patches appear less suitable for murrelets (e.g., Desolation Sound, southeastern Vancouver Island).

Landscape-level analyses using a variety of methods report negative associations of murrelet detections or measures of suitable habitat with elevation in BC (Rodway et al. 1991, 1993a,b), Washington (Hamer 1995) and Oregon and California (Meyer 1999, Meyer and Miller 2002). Watershed-level radar studies show strong correlations with low-elevation old-growth forest below 600 m (Burger 2001, Manley 2000) or below 1067 m (Raphael et al. 2002) and weaker correlations with higher elevations or with the full range of forests (section 4.5.3). Drever and Kaiser (1999) reported a weak negative relationship between murrelet counts and low elevation forest (<300 m), but the poorly defined, multi-drainage catchment areas in this study reduce its predictive value.

In conclusion, nest distributions, evidence of occupancy, the distribution of essential tree characteristics, and radar counts all suggest that low elevation forests provide the most suitable nesting habitat. There is no obvious elevation cut-off point but most indicators suggest sharp declines in habitat suitability and use above 900 or 1000 m. Some data suggest that old growth forest below 600 m is most suitable in more intact watersheds. Until more data are available it seems reasonable to use 0-900 m as the range of the most suitable habitat in most areas. This range covers the elevations for most nests in Desolation Sound where nest success increased with elevation. Many biogeoclimatic boundaries in the coastal forests are set at 900 or 950 m (Green and Klinka 1994), making this a convenient management boundary. The 900-1500 m range could be considered less suitable, but still likely to support a small portion of the murrelet population. Habitat above 1500 m could be considered unsuitable, unless there is evidence to suggest the murrelets are using it (e.g., nests or occupancy).

It is risky to use elevation alone as an indicator of suitable habitat. Other habitat indicators, such as tree size and the relative density of platform limbs, need to be considered in conjunction with

elevation. The tentative boundaries suggested above could be modified with local information, because elevational effects are likely to vary with latitude, aspect and slope. Ideally, regionally specific algorithms, which have been tested and refined in field studies should be used to identify suitable habitat.

4.9 Effects of slope, aspect and topography

As with much of the data on murrelets, there are no consistent indicators of how murrelets respond to slope and topography. The data from nests found by telemetry has convincingly shown that murrelets frequently nest on steep slopes, and in Desolation Sound breeding success increased with slope of nest sites (section 4.5.1). There is thus no reason to ignore steep areas in habitat management, providing there is evidence of nesting, suitable habitat or occupancy. It is not clear, however, whether steep slopes necessarily provide the best habitat in situations where there is still suitable habitat available on valley bottoms or gentle slopes. Studies made in areas where such habitat exists (Clayoquot Sound, Carmanah-Walbran, Queen Charlotte Islands/Haida Gwaii) tend to show negative or non-significant associations between slope and murrelet occupancy or measures of nesting micro-habitats (sections 4.3, 4.5.2, and 4.6.2). Even in the Desolation Sound area, Manley (1999) reported significant negative effects of slope when comparing stands with and without evidence of occupancy.

Steeper slopes are presumed to provide some benefit to murrelets by making it easier for them to access the mid- to lower-crowns of the trees, where larger branches occur. This idea has not been critically tested but is a reasonable assumption. Gaps in the forest canopy provide access to mid-to lower-canopy limbs regardless of slope, and gaps and variable canopy structure are characteristic of old-growth nesting sites in contiguous forest. Slopes are therefore not essential if canopy structure is variable as in most old-growth forest. Another possibility is that steep slopes have lower densities of predators. This has not been tested.

Given the apparent contradiction in data on slope, it seems prudent to avoid using slope as a strong predictor (+ve or -ve) of suitable habitat in BC. Instead, management and mapping should focus on forest structure, measures of canopy accessibility, and nest site attributes known to be reliable indicators (e.g., presence of platform limbs and epiphyte cover). If local studies indicate evidence of nests, occupancy, or suitable habitat in steep areas being considered as protected areas, then these should be included. Slope and/or position within the valley topography have not been included in most algorithms developed for identifying suitable habitat.

Few studies have seriously addressed the effects of aspect on murrelets and their nest habitat. In drier areas such as parts of the Sunshine Coast and East Vancouver Island, forests on southfacing slopes sometimes have little moss cover and fewer suitable platforms for nesting (B. Smart, D. Dunbar and A. Burger, unpubl. data), but in moister areas aspect seems less important. Further analysis is clearly needed on this topic.

5 MARINE HABITAT

5.1 Marine Habitat Characteristics

Marbled Murrelets spend most of their lives at sea, and are influenced by changes in marine ecosystems which need to be considered in a conservation and management plan. It is difficult, however, to generalize about marine habitat preferences of Marbled Murrelet, because of the variability in the distribution of the birds and the factors that affect them, and the scarcity of detailed studies at sea. One problem is that seabirds respond differently to environmental variables at different spatial and temporal scales (Hunt and Schneider 1987), and this is seldom considered in studies of Marbled Murrelets. A significant correlation at spatial scales of 1 km might not be evident at spatial scales of 10 km. The same is true for variations in temporal scales (seconds to decades). Murrelets show strong diurnal and seasonal variations in their distribution at sea (Carter and Sealy 1990, Rodway et al. 1995, Gaston 1996, Lougheed 2000, Speckman et al. 2000) which can mask patterns in habitat use if the study protocol does not take them into account.

Predictability of murrelet distributions at sea – Several studies have reported predictable aggregations of murrelets at favoured feeding sites within study areas over several years. These include Desolation Sound (Kaiser et al. 1991, Lougheed 2000, Bradley 2002), Clayoquot Sound (Sealy and Carter 1984, Kelson et al. 1995, Mason et al. 2002), Barkley Sound (Carter 1984, Carter and Sealy 1990) and the West Coast Trail coast (Burger 1997b) in BC, and several studies outside BC (Kuletz 1996, Speckman et al. 2000, Miller et al. 2002). By contrast, Strong et al. (1995) found significant shifts in distribution along the entire Oregon coast from year to year. There have been relatively few detailed studies of the physical and biological factors which might explain spatial and temporal distributions, and allow predictions of "good" marine habitat. Some of these are reviewed below.

Distribution relative to shore – On exposed shores in BC murrelets tend to remain within 0.5 km of the shore, but in sheltered waters among islands or in inlets they might occur 1-2 km or more from shore (Sealy 1975a, Carter 1994, Burger 1995a, Gaston 1996). In Oregon and California murrelets appear to use a broader nearshore zone along exposed shores, but are usually within 1 km of the shore (Strong et al. 1995, Becker et al. 1997) or 2 km (Ralph and Miller 1995). They tend to avoid the centres of deep fjords and channels (Carter and Sealy 1990, Burger 1995a). Marbled Murrelet are known to herd schools of fish against the shoreline (Day and Nigro 2000), and to move into sandy shallows to catch sand lance at high tides (Speckman et al. 2000).

Distribution relative to substrate and topography – Carter (1984) found that murrelets aggregated over a glacial sill at the mouth of Trevor Channel in Barkley Sound, BC. This area had concentrations of immature herring and sand lance, associated with thermal fronts and gravel/sand substrates. Sand or gravel substrates providing habitat for sand lance are likely to be important predictors of localized murrelet distribution. This was evident along the exposed West

Coast Trail coast south of Barkley Sound, where murrelet densities were positively correlated with shoreline sand and gravel areas (Burger 1997b). Day and Nigro (2000) also found a significant effect of shoreline substrate on murrelet densities in Prince William Sound, Alaska.

Water depth – Marbled Murrelets usually forage in water less than 30 m deep but can be found in deeper water (Sealy 1975a, Carter and Sealy 1990, Gaston 1996, Day and Nigro 2000). See section 2.4 for foraging depths.

Tides and currents –Murrelets typically forage in relatively sheltered waters. Several studies have found no apparent effect of tides on the distribution and foraging behaviour of murrelets (Carter and Sealy 1990, Kaiser et al. 1991, Day and Nigro 2000). Speckman et al. (2000) found a significant effect: murrelet counts in Auke Bay, SE Alaska were highest at high or falling morning tides. Murrelets seem attracted to sites with strong tidal flow in some areas, but not others (reviewed by Burger 1995a). Day and Nigro (2000) found that Marbled Murrelets in Prince William Sound, Alaska were common at tidal rips but murrelet abundance overall was not affected by current speed. Kaiser et al. (1991) found murrelets aggregated in strong currents during the latter half of the breeding season (6 June to 8 August) which were also areas of clear, colder water in which sand lance were more likely to be found.

Sea temperature - Murrelets respond to temperatures which affect the productivity, concentrations and depth of their prey. These relationships of murrelets, prey and sea surface temperature (SST) are complex and strongly affected by the spatial and temporal scale at which they are considered. For example, Speckman et al. (2000) found a negative correlation between murrelet abundance and SST during egg-laying and incubation, but in some years there were positive correlations later in the season. At a larger time frame, they found that cold local temperatures in 1992 reduced local productivity, leading to lower murrelet densities and reduced chick production relative to 1993. In Desolation Sound, Kaiser et al. (1991) reported no significant effects of SST on murrelet counts except late in the season. In the same area Lougheed (2000) found a significant negative correlation between SST and murrelet numbers in two warm years but not in a third cooler year; murrelets avoided water >17°C. Near glaciers murrelets avoided the coldest water (3°C) but showed no further preferences for temperatures 4-17°C (Day and Nigro 2000). Off southwest Vancouver Island, murrelet densities showed no trends with SST (Burger 1997b). On some surveys their prey densities were positively correlated with SST at scales of 0.25-0.5 km but not at larger spatial scales. Annual variations in at-sea and inland counts of murrelets in this area showed some negative effects of warm oceans (Burger 2000).

Sea salinity – This is usually measured as sea surface salinity (SSS). Salinity, like temperature, has complex relationships with murrelet densities and distribution at sea. In Desolation Sound, Kaiser et al. (1991) found a weak positive correlation with SSS, whereas Lougheed (2000) reported a weak, negative effect in one of three years. Burger (1997b) found no effect from SSS off Vancouver Island. In Prince William Sound, Alaska, Day and Nigro (2000) found that murrelets were either attracted to low salinity (11-17 ‰) near freshwater runoff, or high salinity (25-30 ‰) near the mouths of bays.

Coarse-scale modeling – Yen, Huettmann and Cooke (in prep.) are preparing a coarse-scale model (>10 km spatial scale) to explain the at-sea densities and distribution of Marbled Murrelet along the entire British Columbia coast. At present their model parameters include sea surface temperature, tidal current, herring spawn data, distribution of sand and fine gravel substrates as a predictor of sand lance distribution, location of glaciers, and inland distribution of old-growth forests. If reliable predictors of murrelet densities can be modeled from such data, then the model will be useful in predicting the densities and distribution of murrelets in areas not yet surveyed. The model will also be useful to map areas where the marine parameters predict there should be large populations, but loss of inland nesting habitat might be limiting the present populations.

A large-scale analysis of nine regions (2121-6504 km² in area) in northern California and southern Oregon found that murrelet densities at sea were not well explained by marine habitat measures, but were strongly associated with the areas, patch size and contiguity of old-growth forest inland (Miller et al. 2002). Unexpectedly, availability of highly productive, nutrient rich marine habitats explained less than 5% of the variation in murrelet numbers at sea at the regional level. At a smaller landscape scale, inland habitats most used by murrelets were generally close to ocean bays, submarine canyons, river mouths, sandy shores, and ocean areas with high primary productivity (Meyer 1999). Rocky shores were less preferred than sandy shores. Meyer (1999) stressed the need to consider both inland forests and productive marine habitat in management plans.

5.2 Diurnal variations in marine habitats

Diurnal shifts in the distribution and foraging behaviour of Marbled Murrelets have been reported from many areas (Sealy 1975a, Carter and Sealy 1990, Rodway et al. 1995, Day and Nigro 2000, Lougheed 2000, Speckman et al. 2000). In general the adults appear to do most feeding in the morning, and in many areas move to different locations in preparation for going inland at dusk or catching larger prey for delivering to their chicks. Most studies report movements closer to inland nesting areas in the late afternoon.

5.3 Seasonal variations in marine habitats

Seasonal shifts in the densities, distribution and foraging behaviour are also the norm (Sealy 1975a, Carter and Sealy 1990, Rodway et al. 1995, Burger 1995a, Day and Nigro 2000, Lougheed 2000, Speckman et al. 2000). Such changes are due to several factors including different arrival times of breeding adults and immature birds, more restricted foraging ranges during chick-feeding than during egg production and incubation, post-breeding movements to moulting areas

5.4 Long-term variations – regime shifts, El Niño and global warming

Multi-year cycles and long-term changes in ocean environments affecting seabirds operate at several overlapping spatial scales. Periodic warm (El Niño) and cold (La Niña) ocean conditions in the northeast Pacific occur at intervals of 3-7 years and are linked with the El Niño – Southern Oscillation (ENSO) processes generated in the tropical Pacific. El Niño events tend to have negative effects on seabirds in the northeast Pacific (Hodder and Greybill 1985, Wilson 1991, Bertram et al. 2001).

Larger scale Pacific Decadal Oscillations (PDO), operating at scales of about 20 years have recently been recognized (Piatt and Anderson 1996, Francis et al. 1998, McGowan et al. 1998, Anderson and Piatt 1999). Changes in temperature and currents create "regime-shifts" which can affect entire pelagic food webs. In the greater Gulf of Alaska, including BC, there was a major shift to a "warm" phase (warm in the eastern part of the gulf) that began around 1977 and persisted until about 1999. Fish-eating seabirds in many areas were negatively affected by this change, particularly by the reduced availability of lipid-rich species (e.g., capelin), as conditions favoured less fatty groundfish species (e.g., juvenile walleye pollock *Theragra chalcogramma*)(Piatt and Anderson 1996, Anderson and Piatt 1999).

Finally, at an even larger time scale there is evidence of global climate change, which appears likely to create warmer conditions in the Pacific Northwest.

The impacts of these multi-year cycles and trends on Marbled Murrelets are not clear and there are few long-term data series to test these effects. Even the impacts of El Niño events are not obvious (Ralph et al. 1995b). In Prince William Sound and Katchemak Bay, Alaska, the intensive research triggered by the *Exxon Valdez* oil spill has provided some evidence that Marbled Murrelets were negatively affected by the marine conditions during the 1977-1999 PDO phase (details in the next section). Because they forage primarily in nearshore waters, murrelets might be more strongly affected by local marine processes (tidal flow, freshwater runoff, fine-scale upwelling etc.) than by the larger-scale pelagic processes. Understanding the responses of Marbled Murrelet to oceanic processes is important in order to determine whether population trends are caused by food availability at sea or loss of nesting habitat inland.

5.5 Limiting factors at sea

About 98% of seabird species and a higher proportion of seabird populations are colonial (Furness and Monaghan 1986). Populations of these species are sometimes limited by available nest sites at colonies, but many populations appear to be limited by the availability of food during the breeding season (Birkhead and Furness 1985, Croxall and Rothery 1991, Cairns 1992). Large colonies of seabirds are usually located near highly productive marine areas, providing large patches of prey within commuting distance of the colonies. Marbled Murrelets differ from this general seabird pattern in that they are not colonial and have a widespread breeding distribution,

with relatively low densities compared with most colonial seabirds. It seems likely that they evolved this non-colonial nesting behaviour in response to two major factors: the availability of nest sites on large trees across a huge latitudinal range (Alaska through central California), and the ability to exploit small, dispersed patches of prey in nearshore waters. The low nest density and the scattered marine distribution of Marbled Murrelet suggest a species that exploits spatially dispersed prey (Carter and Sealy 1990, Ostrand et al. 1998). Such prey might be too ephemeral to support large colonies of birds forced to forage near the colony while breeding. In many parts of their range Marbled Murrelets nest in areas where there are no suitable islands or cliffs to support large populations of colonial seabirds.

Factors limiting populations of Marbled Murrelet are therefore likely to differ from those limiting their colonial cousins. There have been no definitive studies on limiting factors of murrelet populations. In their overview, Ralph et al. (1995b) concluded that populations through much of the southern range are now limited by available nesting habitat (i.e., old-growth trees), but they suggested that population size in some northern areas might be determined by the availability of prey at sea. Support for this latter idea comes from the research done in Prince William Sound, Alaska, where Marbled Murrelets are the most common seabird. This population has declined since 1972 (Agler et al. 1998), and has not shown any recovery after about 8000 murrelets were killed in the 1989 Exxon Valdez oil spill (Kuletz 1996, Irons et al. 2000, Lance et al. 2001). This is attributed to the combined effects of the oil spill and to changes in the availability of prev (Kuletz 1996, Kuletz et al. 1997, Irons et al. 2000). There has been little logging or other loss of nesting habitat around Prince William Sound. Other piscivorous seabirds have also declined in this area over the same period (Kuletz et al. 1997, Irons et al. 2000, Agler et al. 1999). Changes in prey availability are probably associated with the regime shifts affecting the entire Gulf of Alaska (Piatt and Anderson 1996, McGowan et al. 1998, Anderson and Piatt 1999). The actual processes acting to limit Marbled Murrelet populations are still being investigated (K. Kuletz, pers. comm.).

It is possible, although untested, that local populations of murrelets in parts of BC might also be limited by prey availability. The negative effects of warm ocean conditions found off southwest Vancouver Island (Burger 2000), although inconclusive, suggest some influence of prey availability on local densities and breeding activity. Additional research to determine the relative effects of marine and inland factors on murrelet populations in both modified and relatively pristine parts of BC would help focus management and conservation priorities.

6 STATUS OF MARBLED MURRELETS AND POSSIBLE THREATS

6.1 Status of Marbled Murrelets in North America

United States – The Washington, Oregon and California populations were federally listed as threatened in 1992, due to the high rate of loss and fragmentation of the nesting habitat, and mortality associated with oil spills and net fisheries (U.S. Fish and Wildlife Service 1997). Critical habitat was designated in 1996 (U.S. Fish and Wildlife Service 1996). Within each state, the species is listed as endangered in California and threatened in Oregon and Washington. The status of the Alaska population is under review.

Canada (British Columbia) – See the introduction to this report.

6.2 Threats to Marbled Murrelets in British Columbia

6.2.1 Background

Marbled Murrelets are of conservation concern for several reasons (Hull 1999):

- most murrelets nest in old-growth forests and this habitat is disappearing due to logging and development;
- they are detrimentally impacted by fragmentation of forests, probably because of an increase in the rate of predation;
- they forage in the inshore marine habitat which is close to human development and sources of pollution; and
- they have a very low recruitment rate, which means that populations remain stable only if adult survival rates are high.

6.2.2 Demographic

Threats to adults tend to be in the marine environment, including natural processes such as predation from eagles and starvation, and human activities such as oil spills, gill-nets and anthropogenic changes to prey stocks. Population models show that murrelet populations are most susceptible to adult survival (Beissinger and Nur 1997, Boulanger et al. 1999), which means that marine risks, while relatively rare, can have significant impacts on populations. Adult survival can also be affected by increased predation risk at forest sites, in addition to loss of eggs or chicks. although the primary risks inland are to eggs and chicks and hence affect recruitment or fecundity rather than adult survival. Forest fragmentation seems to negatively impact nesting success. Most research on the effects of inland predators have focused on nest predators and the subsequent effects on fecundity, but the more difficult task of assessing adult mortality in fragmented and intact forests is needed to fully understand the demographic impacts of forest fragmentation.

6.2.3 Genetic

In any widespread species like the Marbled Murrelet there is a risk that local extinctions can reduce genetic diversity. The available evidence suggests that there is relatively little genetic variation and some gene flow among populations across the North American range, apart from divergence of the small population in the outer Aleutian Islands (see section 2.1). These tests were, however, focussed on selected alleles and did not include all possible local populations and the possibility remains that there might be important genetic sub-populations.

6.2.4 Biological threats (disease, parasites, predators, competitors etc.)

Disease and parasites - There is little information on the impacts of disease or parasites on murrelets. Being non-colonial they are probably less susceptible to these problems than most other seabirds. Two juvenile Marbled Murrelet were among the many birds killed by paralytic shellfish poisoning in Pacific Rim National Park, Vancouver Island in 1989 (MacBean 1989). Thousands of dead sand lance washed ashore at the same time, which were highly toxic.

Predators – Predation appears to be the most significant factor affecting breeding success and hence fecundity in murrelets. Details on predators are given in the General Biology description (section 2.7), and the risks of predation associated with forest fragmentation are discussed in section 4.7.

Competing species – There is considerable dietary overlap between Marbled Murrelets and other sympatric seabirds, especially Common Murres (Uria aalge) and Rhinoceros Auklets (Cerorhinca monocerata) (Vermeer et al. 1987, Burkett 1995). Small schooling fish, especially sand lance and juvenile herring, and large crustaceans are important to all three alcids in BC. The effects of competition on murrelets are not known, but murrelets, being the smallest member of the fish-eating alcid guild, are likely to experience competitive exclusion at some prey schools. Larger alcids, especially Common Murres, are known to disrupt feeding in smaller alcids (Chilton and Sealy 1987, Piatt 1990). Such interactions are thought to explain the low numbers of Marbled Murrelets in mixed-species feeding flocks in areas where there are many murres and other large alcids, such as the west coast of Vancouver Island. Murrelets commonly forage in mixed-species flocks with gulls in places where there are few large alcids, such as Desolation Sound (Mahon et al. 1992). It seems unlikely, however, that such interactions actually cause exclusions of murrelet populations from potential breeding range; some of the highest densities of breeding murrelets occur off southwest Vancouver Island where there are substantial numbers of murres and Rhinoceros Auklets in summer (Burger 1995a). Most of the large colonies of murres, auklets and puffins are on offshore islands off Cape Scott, and in Queen Charlotte Strait and Hecate Strait (Rodway 1991), where there appears to be little likelihood of competition with Marbled Murrelets.

Murrelets might be negatively affected by competition with predatory fish species. During warm water years in the 1990s large schools of mackerel (*Scomber japonicus*) and jack mackerel

(*Trachurus symmetricus*) invaded Barkley Sound and adjacent seas and decimated stocks of juvenile salmonids and juvenile herring (B. Hargreaves pers. comm.). This was believed to have contributed to reduced local numbers and breeding activity in Marbled Murrelet during warm years (Burger 2000).

Intraspecific competition - Low nest densities, linear correlations between area of old-growth forest and numbers of murrelets all suggest that there is some spacing behaviour, perhaps territoriality occurring in the forest. This would be consistent with the high frequency of vocalization and sometimes even physical attacks which occur at dawn over suitable forest habitat.

Introduced and invasive species - Murrelets do not appear to be affected by any introduced or invasive species in their marine habitat, apart from the mackerel discussed above. This also appears true for most of their nesting habitat, except for the Queen Charlotte Islands, where introduced red squirrels are likely to have caused some increase in predation. In addition, the availability of squirrels is likely to have caused an increase in populations of marten, which might subsequently also take more murrelets.

6.2.5 Changes in prey populations

Marine food webs are affected by complex interactions involving a wide range of physical, chemical and biological processes which are ultimately linked to local, regional and global climate processes. Marbled Murrelets, like other upper-trophic level consumers, are susceptible to changes in these processes at variable spatial and time scales, which are not well known.

Marbled Murrelets take a wide range of prey types which should give them some adaptability to changing prey stocks. There is some circumstantial evidence that murrelets from southwest Vancouver Island were negatively affected by warm ocean conditions in the 1990s, and this might have been driven by changes in prey availability as described above (Burger 2000).

6.2.6 Forestry, agriculture and urban development

Forest management - The most significant threats to murrelets resulting from forest management are direct loss of nesting habitat and the effects of fragmentation. These are discussed in detail above in section 4. Fire and insect damage to potential nest trees are additional risks, but neither appear to be common in the coastal forests in which murrelets breed.

Urban and agricultural development – Clearing of forest for urban and agricultural development undoubtedly removed large tracts of suitable nesting habitat, especially in the Fraser Valley and on the eastern side of Vancouver Island. Such development was almost certainly partly responsible for the declines in murrelet numbers observed in the early 20th century in the Strait of Georgia (Brooks 1926, Pearse 1946). The extent to which this development still threatens remaining suitable habitat is not known. Urban and agricultural development likely pose considerably less threat to murrelets than industrial forestry operations, but their effects are more permanent and irreversible.

6.2.7 Fishing, fishery by-catch and aquaculture

Changes in prey stocks due to fishing - Of the common prey items taken by Marbled Murrelets, only herring are commercially exploited on a large scale in BC. Herring populations were seriously depleted through over-fishing in the 1960s in many parts of BC, but the impacts on bird populations were not studied. Herring stocks have recovered in some areas but remain low in other areas, and the effects of herring availability on Marbled Murrelets should be assessed in more detail. There do not appear to be plans yet for widescale fishing of sand lance or other prey fish species to produce fish-meal, as occurs in other parts of the world. There have been a few experimental fisheries for euphausiids, and there is still a chance that this fishery may develop as a source of food for pen-reared salmon. An intensive euphausiid fishery might affect murrelets directly, since they eat large euphausiids, or disrupt the food webs on which they depend.

Gill-nets – Mortality from gill-nets may be one of the greatest threats to Marbled Murrelet populations in many parts of Alaska, BC, and Washington, although this has seldom been studied (Ralph et al. 1995b, Carter et al. 1995, Hull 1999, Melvin and Parrish 2001). Many murrelets were killed by nets off California in the 1970s and 1980s, but with new regulations banning or restricting gill-nets, mortality is probably negligible off California and also Oregon (Nelson et al. 1992, Carter et al. 1995). Mortality in salmon gill-nets in Alaska is estimated at 3300 Marbled Murrelets per year, based on observer program data and extrapolations using fishing permits and fishing effort data (Piatt and Naslund 1995).

Seabird by-catch in gill-nets and seiners is a serious problem in Washington, especially in Puget Sound, primarily affecting Common Murres and Rhinoceros Auklets (Melvin et al. 1999, Melvin and Parrish 2001), but also posing a threat to Marbled Murrelets (Carter et al. 1995). The risks of these fisheries to murrelets prompted considerable observation effort and research on methods to reduce the by-catch. Most studies found very low catches of Marbled Murrelets, mainly because there were few murrelets in the fishing grounds at the time of the fishing (Pierce et al. 1994, Melvin et al. 1997, 1999). For example, during the sockeye gill-net fishery in Puget Sound in 1996, Marbled Murrelets comprised 0.07% (12/17,900) of the seabirds seen near fishing operations, 0.20% (7/3498) of birds encountering nets, and 0.29% (1/349) of birds entangled (Melvin et al. 1997).

In BC the rates of capture, spatial and temporal distribution of mortality, risks of various fishing gear, and effects on seabird populations by fisheries by-catch are virtually unknown, although these topics are now the focus of research by the Canadian Wildlife Service and the Department of Fisheries and Oceans (K. Morgan and J. Smith, pers. comm.). Areas of the BC coast where gill-netting activity is common have been identified by Carter et al. (1995) and Burger et al. (1997b), but fishing effort changes frequently from year to year making it difficult to predict where problems might arise.

The only detailed study on gill-net mortality done in BC was by Carter and Sealy (1984), who reported a large by-catch of Marbled Murrelets during salmon gill-netting in Barkley Sound in

1979-1980. They estimated a minimum of 175-250 murrelets were killed in 1980, which represented 6.2% of the local breeding population, or 7.8% of the potential fall population (taking into account the additional loss of chicks whose parents had died). Most mortality occurred at night at depths of 2.0-8.5 m. Approximately 90% of the dead birds were breeding adults, 5% non-breeding and 5% hatching-year birds. Gill-netting of this intensity which overlaps with the time of maximum numbers of murrelets (April-August) is now rare in Barkley Sound, although some by-catch mortality continues (Carter et al. 1995, A. Burger, pers. obs.). In the 1980s and early 1990s there were typically 400 gill-net vessels fishing 24 hours per day on the BC coast, 1-4 days per week, but since the mid- to late-1990s the effort has been about 100 gill-net vessels fishing in daylight only for 1-2 days per week (data from Laurie Gordon, Department of Fisheries and Oceans [DFO], Port Alberni, pers. comm. to J. Smith).

Most of the intensive gill-net fishing off the west coast of Vancouver Island occurs from August to November (Carter et al. 1995), when murrelet densities tend to be fairly low (Burger 1995a). Consequently, there is little evidence of high mortality of Marbled Murrelets in this fishery, although data are sparse. Bird by-catch was recorded during a gill net test fishery for chum salmon off Nitinat Lake, southwest Vancouver Island, in late September to early October, 1995-2000 (J. Mitchell, DFO, unpubl. data). In 6 years this test fishery used 4-8 vessels and made a total of 5,288 sets totalling 10,021 net-hours. In total, 367 birds were caught and 348 birds killed. By-catch rates varied greatly among the years but averaged 0.072 ± 0.049 (SD) birds per set (range 0.039-0.169) or 0.042 ± 0.034 birds per net-hour (range 0.019-0.108). Out of 270 identified birds, six were recorded as Marbled Murrelets (i.e. 2.22%). An additional 97 birds were unidentified, so 6 was the minimum mortality, but a few of the birds recorded as Marbled Murrelet in some years might have been other species misidentified (J. Smith pers. comm.). Most (89 %) of the identified birds were Common Murres. If we assume that 2.22% of the birds were Marbled Murrelets, then the estimated rate of mortality in this test fishery would be $0.016 \pm$ 0.011 (SD) murrelets per set, or 0.009 ± 0.007 murrelets per net-hour. Test fisheries probably do not reflect mortality rates in commercial openings. More vessels are present in the latter fishery, which may cause fewer birds to remain in the area, resulting in lower by-catch rates. On the other hand, commercial vessels generally do not use gear that might reduce fish by-catch (e.g. drop weed-lines, Alaska twist), some of which might also reduce incidental seabird mortality (J. Smith pers. comm.).

There has been intensive research effort in Washington over several years to develop gill-netting methods which will reduce by-catch without significantly reducing salmon catches (Melvin et al. 1997, 1999). Marbled Murrelets were rare in this experimental fishery (1 bird caught in 642 sets, compared with 258 Common Murres and 85 Rhinoceros Auklets), but the methods developed to reduce by-catch are probably applicable to murrelets. Most birds and few fish were caught in the upper quarter of the nets (0-4.6 m deep), and the most successful modifications were to increase the visibility to birds of these net panels. Additional reductions were obtained by restricting the fishing to daylight hours (most murres and auklets were caught at dawn and dusk), and by reducing the seasonal overlap between fishing and bird aggregations on the fishing grounds. A combination of net modification, daytime fishing and seasonal modifications could lead to reductions of bird by-catch by 70-75% in this gill-net fishery in Washington (Melvin et al. 1999).

Similarly in BC, eliminating night and crepuscular gill-netting seems to have reduced by-catch in the chum fishery off southwestern Vancouver Island. Currently DFO is testing gill-nets with no mesh in the upper 2 m, as well as other modifications aimed at reducing by-catch of marine mammals and sockeye salmon, but which are also likely to reduce seabird by-catch (J. Smith, pers. comm.).

Simulation models have shown that adult survival is the most sensitive demographic parameter affecting populations of Marbled Murrelets (Beissinger and Nur 1997, Boulanger et al. 1999) and many other seabirds (Nur and Sydeman 1999). Field studies show that most murrelets killed by gill-nets are breeding adults (Carter and Sealy 1984, Carter et al. 1995). Even a low rate of mortality can therefore cause or contribute to a decline in local populations. Beissinger (1995b) modelled the impacts of gill-net mortality on population viability of Marbled Murrelets, by modifying his general population model for the species (Beissinger 1995a). The goal was to determine how gill-net mortality might exacerbate the population declines which were predicted by the general model. Beissinger (1995b) found that even a modest level of gill-net mortality was likely to impact murrelet populations. This can be seen in the projected time to extinction of a population with different by-catch levels (Figure 6.1). These simulations are not meant to be taken literally, but are meant to illustrate the relative risks associated with likely levels of by-catch. A similar simulation model showed that an increase in adult mortality of 3-5% was sufficient to cause a population decrease in Common Murres (Nur and Sydeman 1999).

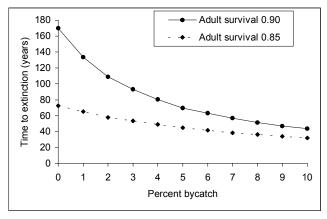


Figure 6.1. Effects of bycatch levels, measured as a percentage of the population killed annually, on the time to extinction. The population was set at 2600 birds (approximate population in Puget Sound and Strait of Juan de Fuca), and adult survival was set at 0.90 and 0.85 in the two simulations. From Beissinger (1995b).

In summary, the available evidence suggests that risks of widespread and significant mortality to Marbled Murrelets from gill-nets are low in BC, but there are too few data to be complacent. The high mortality recorded in Barkley Sound in 1979-1980 (Carter and Sealy 1984), and the strong impacts of by-catch in population simulation models (Beissinger 1995b, Boulanger et al. 1999) are reminders that murrelets are highly vulnerable to this fishery, but it is not known whether by-catch is a serious problem in BC.

Purse-seiners – Two Marbled Murrelets were entangled in seine nets in Washington during a pilot study (Pierce et al. 1994). Purse-seine fisheries in Barkley Sound killed hundreds of

Common Murres in 1979-1982, but occurred in areas with few Marbled Murrelets, and no dead murrelets were recovered from this fishery (Carter et al. 1995). Purse seining in areas with high murrelet concentrations might cause significant mortality, but again there are too few data to make any conclusions on its impact.

Sports fishery - There are anecdotal reports of Marbled Murrelets hooked on sports-fishing lures off Campbell River, in Barkley Sound and in Clayoquot Sound (Campbell 1967, Carter et al. 1995, J. Kelson pers. comm., A. Burger, pers. obs.). Many of these birds are released alive, but may suffer mortal injuries when removed from hooks. The numbers of birds caught and the likely impact of this fishery in BC remains unknown, but requires investigation in areas where there is overlap between sports fishing areas and murrelet concentrations (e.g., in Barkley, Clayoquot, and Desolation sounds, and off Queen Charlotte Islands/Haida Gwaii).

Aquaculture - Marbled Murrelets are likely to be negatively affected by shellfish and finfish farms when these facilities are built in sheltered waters normally used for foraging and resting by murrelets. Disturbance from people and boats is the greatest problem, although there might also be highly localised reductions in prey due to fecal pollution from finfish facilities (Vermeer and Morgan 1989). Potential conflicts between seabirds and aquaculture through disturbance and habitat changes were identified in Sechelt-Sunshine Coast, Campbell River-Desolation Sound, Barkley Sound-Alberni Inlet, Clayoquot Sound, Kyuquot Sound, and Queen Charlotte Strait, but in most of the coast it was difficult to assess the degree of interference (Booth and Rueggeberg 1989, Rueggeberg and Booth 1989). Marbled Murrelets are common in all of these identified areas, either seasonally or year-round.

6.2.8 Oil spills

Seabirds are at risk to oil in many forms, including crude, bunker, diesel, gasoline and vegetable oil, resulting from both large catastrophic spills, like the *Exxon Valdez* spill, as well as the numerous, small and often undocumented spills. Fouling of plumage is the most obvious consequence of birds encountering oil, but birds are also killed or debilitated by the highly toxic compounds in most types of oil, ingested while trying to clean themselves (Leighton 1991, Burger and Fry 1993, Carter and Kuletz 1995). Some of the sub-lethal effects may persist for several years through physiological impairment or disruption to pair bonds. The risks and actual mortality from catastrophic and chronic oil spills to seabirds in BC were reviewed by Burger (1992) and Burger and Fry (1993), but these data are likely to be somewhat out of date. On the one hand there has likely been an increase in the volume and rates of shipping in BC waters, but perhaps balanced by improved handling and shipping techniques, increased vigilance, and better monitoring of oil pollution.

Because they remain on the sea for most of their lives, forage by diving, and prefer nearshore habitats (usually <1 km offshore), Marbled Murrelets were in the highest rank of vulnerability to oil spills any species of seabird in Alaska (King and Sanger 1979), and the Pacific Northwest (Carter and Kuletz 1995).

Marbled Murrelets have been killed in numerous large oil spills (Carter and Kuletz 1995). The most significant was the *Exxon Valdez* spill in Alaska which killed approximately 8400 murrelets (Piatt and Naslund 1995). Recent major spills affecting BC murrelets included the *Nestucca* spill, which killed at least 145 Marbled Murrelets off northern Washington and Vancouver Island (Burger 1993b), and the *Tenyo Maru* spill at the entrance to the Strait of Juan de Fuca which killed at least 45 murrelets and likely many more (Carter and Kuletz 1995). These are almost certainly underestimates, because the small carcasses of murrelets are easily missed in clean-up operations.

The risks of large, catastrophic spills within areas used by murrelets in BC are high. Annually in the early 1990s there were more than 7000 transits of freighters and tankers in British Columbia's waters, including at least 1500 tanker trips to or from Alaska, and more than 350 loaded tankers entered the Strait of Juan de Fuca (Burger 1992). The volume of shipping is likely higher now. Risk models for southern BC and northern Washington predicted that spills exceeding 1000 barrels could be expected every 2.5 years for crude oil, and every 1.3 years for all petroleum products, with longer intervals between larger spills (Cohen and Aylesworth 1990). The actual frequency of large spills affecting BC between 1974 and 1991 was fairly close to that predicted (Burger 1992).

In addition to well-publicized catastrophic spills, many seabirds are killed by small, often unreported spills. Many hundreds of small spills occur each year in BC, from fishing vessels, recreational craft, marinas and fueling barges (Burger 1992). Monthly beached bird surveys between 1989 and 1992 showed that at least 6% of the beached carcasses were oiled by small chronic spills, and where the cause of death was known, oiling was responsible for at least 30% of all deaths (Burger 1993a). Oiled birds were found in most months, with no apparent seasonal pattern. The highest densities were found on the west coast of Vancouver Island (12.6% of 190 carcasses), southern Vancouver Island (10.3% of 29 carcasses) and in the Strait of Georgia and Gulf Islands (17.4% of 23 carcasses). The mean density of oiled birds (0.02 per km surveyed) was among the lowest in the world, but the high volumes of logs and other wrack on local beaches reduced the chances of finding oiled birds. Marbled Murrelets were not among the oiled birds in this small sample, but should experience similar risks of being oiled as other coastal species, but because they are one of the smallest seabirds their carcasses are likely to be overlooked in beach surveys.

Overall, chronic oil pollution is likely to kill small numbers of Marbled Murrelet in BC each year, but probably has no significant impact on the overall population. The risks from a large catastrophic oil spill, similar to the *Nestucca* (Rodway et al. 1989, Burger 1993b) or *Exxon Valdez* (Piatt et al. 1990) spills, are, however, significant and if such a spill coincided with seasonal aggregations of murrelets it could cause a serious local population decline. Oil spills would kill a large proportion of adult birds, resulting in significant demographic impacts (Boulanger et al. 1999).

6.2.9 Other pollutants, toxicants and plastic debris

Chemical contamination – Marbled Murrelets have not been subjected to research or monitoring on the effects of chemical contamination, but as fish-eating birds relatively high on food chains they are likely to be affected in a similar way to other fish-eating birds living in the same areas. See reviews by Furness (1993), Elliott and Noble (1993), Ohlendorf (1993) and Fry (1995) on the chemical pollutants likely to affect Marbled Murrelets in BC, and Mahaffy et al. (1994) and Nicol et al. (2000) for summaries of the status of these pollutants in the Strait of Georgia. The following is a brief assessment of the chemical contaminants likely to be relevant to Marbled Murrelets in BC.

Dioxins (polychlorinated dibenzo-dioxins - PCDDs) and furans (polychlorinated dibenzo-furans PCDFs) were common in pulp-mill effluent before 1990. These toxins were found in high concentrations of fish-eating Bald Eagles, Great Blue Herons (*Ardea herodias*), and Double-crested Cormorants (*Phalacrocorax auritus*) in the Strait of Georgia, and grebes near Port Alberni (Elliot and Noble 1993). Their main impact is to disrupt embryo development and they were linked with massive breeding failure in some populations of Great Blue Herons. Release of these chemicals from pulp-mills in BC was restricted in 1990, but smaller amounts continue to be released into the sea from other sources (Nicol et al. 2000). Concentrations in the eggs of eagles, herons and cormorants in the Strait of Georgia declined rapidly after 1990, but remain elevated in eagle eggs near contaminated sites (Nicol et al. 2000).

Organochlorine pesticides are now widely banned in most Pacific Rim countries, but these compounds and their breakdown products (including DDT, DDD, DDE, dieldrin, heptachlor, hexachlorocyclohexane [HCH], and hexachlorobenzene [HCB]) continue to be found in the eggs of marine birds in BC (Elliott and Noble 1993, Nicol et al. 2000). Some organochlorines, including DDT, are still used in some Asian countries and affect BC via ocean and air currents (Elliott and Noble 1993). DDE levels in eggs of Double-crested Cormorants and Bald Eagles in the Strait of Georgia now fluctuate close to the levels where production of young begins to decline (Elliott et al. 1996, Nicol et al. 2000).

Polychlorinated biphenyls (PCBs) were widely used in electrical transformers and as additives to paint and ink, before being banned in North America in 1977 (Elliott and Noble 1993). Almost 80% of the PCBs imported into Canada remain in use, stored or are unaccounted for, and PCBs continue to enter marine ecosystems (Nicol et al. 2000). They affect a range of physiological and developmental processes in birds (Elliott and Noble 1993). In the Strait of Georgia, PCB levels in cormorant and heron eggs have declined significantly since the 1970s, and to a lesser extent in those of Bald Eagles (Nicol et al. 2000).

Tributyltin (TBT) and its breakdown products are toxic to wildlife. Used as an anti-fouling agent in marine paint, TBT use is now greatly restricted in BC, but still allowed for larger vessels and by the military (Nicol et al. 2000). Accumulation of butyltins in birds seems restricted to areas near harbours and bio-accumulation via fish seems less likely than via shellfish (Nicol et al. 2000).

Trace elements or heavy metals, notably mercury, cadmium, lead and selenium, have been found in seabirds in concentrations which cause adverse effects to vertebrates, although there are few studies of their effects on seabirds (Ohlendorf (1993). Ohlendorf (1993) concluded that trace elements were unlikely to produce mortality in seabirds in the North Pacific, apart from an isolated situation on Midway Atoll. He cautioned that sampling was sparse and that the interactions of various trace elements was poorly understood in birds.

Although the levels of chemical pollution in the Strait of Georgia seem to have declined since the 1970s and 1980s, these waters and adjacent Puget Sound are among the most polluted marine areas in the range of the Marbled Murrelet (Elliott and Noble 1993, Mahaffy et al. 1994, Fry 1995). These areas support substantial, but depleted populations of Marbled Murrelets, and appear to be the wintering grounds of murrelets which breed elsewhere in BC. Fish-eating mergansers and grebes which winter in the Strait of Georgia show higher levels of contaminants than those wintering in more pristine areas (Elliott and Martin 1998). Concentrations of PCBs were found to increase in fish-eating Western Grebes (*Aechmophorus occidentalis*) during the period the birds were overwintering in Puget Sound (Henny et al. 1990). The concern for Marbled Murrelets in these areas is that they might be subjected to synergistic effects of combinations of contaminants, or subtle sub-lethal effects. Most of the contaminants discussed above can act as endocrine disruptors, which mimic or block the effects of hormones, especially during embryo development (Nicol et al. 2000). The effects of endocrine disruption might not become apparent until the animal reaches maturity, and then suffers impaired breeding.

Plastic debris - Seabirds of the North Pacific frequently ingest plastic (pellets and post-user fragments) mistaken for food items. Although there are few documented cases of ingested plastic harming seabirds, there is concern that large quantities in the gut will impede food intake and digestion, and plastic floating in the ocean absorbs toxins, including PCBs and DDE. No pellets were found in a sample of 61 Marbled Murrelets from Alaska, where there was a high incidence of plastic in gut contents of many other species, including some other alcid species (Robards et al. 1997). Ingestion of plastic seems unlikely to be a problem for murrelets in BC.

6.2.10 Relative significance of threats

It is impossible to assess the significance of the threats reviewed above to Marbled Murrelet populations in BC. Population models indicate that factors affecting adult survival are more likely to impact populations than factors affecting fecundity or immature survival (Beissinger and Nur 1997, Boulanger et al. 1999). Threats to adult survival occur at sea (starvation due to drastic prey declines, natural predation, oil spills, fisheries by-catch) and on land (predation, which might be affected by reduction and fragmentation of forests). This does not necessarily mean that conservation efforts should focus entirely on adult survival, because even if adult survival is high, populations will decline if there is insufficient recruitment (see section 3.1.11). Considerably more information is required on survival, predation, nest success and factors affecting murrelets at sea before the relative significance of the various threats can be accurately assessed. Despite the huge increase in knowledge over the past decade, we are still some way off understanding what limits populations of Marbled Murrelets.

7 ACKNOWLEDGEMENTS

Funding for this review was provided by the British Columbia Ministry of Water, Land and Air Protection (MWLAP), Ministry of Forests (MOF), and Canadian Wildlife Service (CWS). Additional library and logistic support was provided by the University of Victoria. I thank Stewart Guy, Brian Nyberg, Ken Morgan, Myke Chutter, Kathy Paige, Doug Bertram, and members of the Canadian Marbled Murrelet Recovery Team for establishing the framework for the review, setting the priorities, providing guidance and information, and reviewing drafts. Tracey Hooper's bibliography and review of Marbled Murrelet studies from BC, and Cindy Hull's recent COSEWIC review provided valuable starting points for this review. Many people have contributed unpublished data and reports, and reviewed parts or all of the manuscript. In particular I thank the members of the Simon Fraser University /CWS Centre for Wildlife Ecology (director Fred Cooke, and Russell Bradley, Emmanuelle Cam, Mark Drever, Falk Huettmann, David (Dov) Lank, Laura McFarlane-Tranquilla, Nadine Parker, Michael Rodway, Connie Smith, and Peggy Yen) and the following: Volker Bahn, Trudy Chatwin (MWLAP, Nanaimo), Cathy Conroy, Bruce Cousens, Sean Cullen, John Deal (Canadian Forest Products, Ltd.), Vicky Friesen (Queen's University), Tony Gaston (Canadian Wildlife Service, Hull), Tom Hamer (Hamer Environmental), Alton Harestad (SFU), Anne Harfenist, Bill Harper (Osiris Consulting), Norman Holmes, Toby Jones, Gary Kaiser (Canadian Wildlife Service), John Kelson, Kathy Kuletz (U.S. Fish & Wildlife Service, Anchorage), Karl Larsen (University College of the Cariboo, Kamloops), the Laskeek Bay Conservation Society (Queen Charlotte City), Andrea Lawrence, David Lindsay (TimberWest Inc.), Irene Manley, John Marzluff (University of Washington), Michelle Masselink (UVic), Monica Mather, Del Meidinger (MoF), Rick McKelvey (CWS), Carolyn Meyer (University of Wyoming), Kari Nelson (MWALP, Victoria), Kim Nelson (Oregon State University), Deanna Newsom, Martin Raphael (US Forestry Service, Olympia, Washington), Joanna Smith (Birdsmith Ecological Research), Anne Stewart (Bamfield Marine Station), Doug Steventon (MOF, Smithers) and Louise Waterhouse (MOF, Nanaimo). Three anonymous reviewers made many valuable suggestions. I thank Shelagh Bucknell (CWS) for assisting with the layout and publishing.

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9 APPENDICES

9.1 Appendix 1. Counts of Marbled Murrelets at sea in BC

Appendix 1. Counts and population estimates of Marbled Murrelets in British Columbia based on at-sea counts made in May through July.

Area	Mean	Max.	Estimated	Method & notes	No.	Years	Reference
	count	count	population		counts		
West Vancouver Island							
Victoria Harbour to Sooke	-	-	20	Guess	0	-	Burger (this study)
Sooke to San Juan Pt	-	-	200	Guess	0	-	Burger (this study)
Port San Juan (Port Renfrew)	7	10	20	ST, only portion of area	5	91-93	Burger, unpubl.
Owen Point to Cape Beale	2027	2859	3000	ST, inner+outer zones	6	94-96	Burger 1997b
Barkley Sound		3406	3400	GS, likely fewer in 1990s	1	82	Sealy & Carter 1984
Alberni inlet	87	212	300	LT, likely underestimate	4	88	Vermeer & Morgan 1992
Ucluelet to Cox Pt. (Long Beach)		1214	1214	LT, likely fewer in 1990s	1	82	Sealy & Carter 1984
SE Clayoquot Sound	2776	2981	2981	GS, likely underestimate	3	92-96	Kelson & Mather 1999
NW Clayoquot Sound		556	556	GS, likely fewer in 1990s	1	82	Sealy & Carter 1984
Estevan Pt to Bajo Pt. (Nootka Sound)		1103		LT, part of the area	1	99	Manley 2000
Nootka Island							
Ferrer Pt. to Tatchu Pt (Esperanza)							
Tatchu Pt to Kyuquot (Kyuquot Sound)	100			LT, part of the area	9	91	Savard & Lemon 1992
Tatchu Pt to Kyuquot (Kyuquot Sound)		60		LT, part of the area	1	99	Manley 2000
Checkleset Bay	81			LT, part of the area	6	91	Savard & Lemon 1992
Checkleset Bay		128		LT, part of the area	1	99	Manley 2000
Brooks Bay	240			LT, part of the area	5	91	Savard & Lemon 1992
Brooks Bay		65		LT, part of the area	1	1	Manley 2000
Quatsino Sound	6			LT, part of the area	4	91	Savard & Lemon 1992

Cape Parkins to Cape Scott		53		LT, part of the area	1	1	Manley 2000		
Scott Islands	0	0		LT	2	86	Burger 1995a		
Cape Scott to Cape Sutil									
Total West Vancouver Island	See Table 3.4 - based on combination of at-sea counts and radar counts								
Northeast Vancouver Island									
C. Sutil (Goletas Channel) to Port Hardy	112	182		LT, part of the area	3	91	Savard & Lemon 1992		
Port Hardy to Telegraph Cove									
Queen Charlotte Strait	71	105		LT, part of the area	3	91	Savard & Lemon 1992		
Telegraph Cove to Adam River (Johnstone Strait)	68	131		LT, part of the area	3	91	Savard & Lemon 1992		
Adam River to Seymour Narrows									
Seymour Narrows to Campbell River									
Total Northeast Vancouver Island	251	418	500-1000	Total population is a roug	gh estimate	see te	xt.		
East Vancouver Island									
Victoria to Sidney	55	123	200	LT, part of area	15	92-95	J. Clowater, unpubl. data		
Saanich Inlet	5	10	20	LT, along shore	6	86	Morgan 1989		
Gulf Islands			100	Guess			Burger (this study)		
SE Gabriola I to NW Nanoose Peninsula (Nanaimo)	175	200	300	Shore counts		98-00	B. Cousens unpubl. data		
Nanaimo to Baynes Sound;				No data					
Baynes Sound	60	104	104	LT, part of the area	2	91	Savard & Lemon 1992		
Baynes Sound to Campbell River				No data					
Total east coast Vancouver Island	295	437	724	Likely low estimate, given large gaps in coverage. Likely range 700-1000					

Southern Mainland (US border through Bute Inlet)

Boundary Bay to Sandheads

Sandheadsto Point Grey		47	47	LT	2	89	M. Lemon (in Burger 1995a)
Burrard Inlet & Indian Arm		22	22	LT	2	89	M. Lemon (in Burger 1995a)
Pt Akinson to Gower Pt (Howe Sound)		30	30	LT	2	89	M. Lemon (in Burger 1995a)
Gower Pt to Halfmoon Bay (outer coast)				No data			M. Lemon (in Burger 1995a)
Sechelt Inlet				No data			M. Lemon (in Burger 1995a)
Jervis Inlet	85	115	115	LT	2	87	Vermeer 1989
Halfmoon Bay to Powell River (Malaspina Str)				No data			
Powell River to Sarah Point				No data			
Toba Inlet				No data			
Bute Inlet				No data			
Total Southern Mainland	85	214		Total likely 6000-7000 base	d on mar	k-reca _l	oture models and radar counts
				- see text.			
Central Mainland							
Bute Inlet through Princess Royal Channel		3938		LT, sampled 1300 km	1	98	Schroeder et al. 1999
Northern Mainland							
Lareedo Sound to Prince Rupert		285		LT, sampled 326 km	1	90	Kaiser et al. 1991
Kemano to Europaq Bay Hotsprings	30.6	61		LT, sampled 34.5 km	5	92	J. Kelson, unpubl. data
Hotsprings to Weewa	44	85		LT, sampled 36.5 km	5	92	J. Kelson, unpubl. data
Weewa to Kitamaat	23.3	42		LT, sampled 35 km	3	92	J. Kelson, unpubl. data
Kitlope Estuary	30.9	57		Boat, 5 sq. km	9	92	J. Kelson, unpubl. data
Kitlope Lake	5.5	14		Shore count?	14	92	J. Kelson, unpubl. data
Kowesas Estuary	40.7	28		Boat, 6.25 sq. km	3	92	J. Kelson, unpubl. data
	12.7	20		boat, 6.25 sq. kiii	3	32	J. Neison, unpubl. data
Kitlope to Kemano	23.9	68		LT, sampled 27.6 km	16	92	J. Kelson, unpubl. data

Total count for Northern Mainland not tallied since too few areas included. Population estimated from radar counts.

Queen Charlotte Islands/Haida Gwaii

Rose Spit to Skidegate							
Skidegate Inlet/Channel, excluding Long Inlet		90	90	LT part of area	1	90	Rodway et al. 1991
Long Inlet	74	147	147	LT	4	90	Rodway et al. 1991
Sandspit to Gray Bay							
Gray Bay to Cumshewa Hd.		135	135	telescope from shore	1	90	Rodway et al. 1991
Cumshewa Inlet & Selwyn Sd.		30	30	LT	1	77	Vermeer et al. 1983
Skedans to Haswell/Reef Is (Laskeek Bay)	413	1018	1018	LT,	49	91-98	A. J. Gaston, unpubl. data
Louise Is. to Ramsay Is.							
Lyell Is., Darwin Sound & Juan Perez Sound	612	752	2550	LT, extrapolated ~habitat	5	92	French 1993
Skincuttle Inlet, Poole Inlet & Collison Bay	432	528	1161	LT, extrapolated ~habitat	5	91	Lawrence & Backhouse 1991
Skincuttle Inlet to Houston Stewart Channel							
Houston Stewart Channel	17	30	30	Boat counts	3	93	A. Harfenist unpubl. data
Kunghit Is. (excluding Houston Stewart Channel)		185	185	Boat & shore; part of area	-	93	A. Harfenist unpubl. data
Gordon Island to Louscoone Point			44	Boat count	1	93	A. Harfenist unpubl. data
Kunghit Is. to Tasu Sound - Inlets		52	52	LT part of area	1	90	A. Lawrence unpubl. data
West Moresby I. Outer coast		697	697	LT	1	76	Vermeer et al. 1983
West Moresby I. Inlets		24	24	LT	1	76	Vermeer et al. 1983
Tasu Sound		49	49	LT	1	90	A. Lawrence unpubl. data
Tasu Sound to Skidegate Channel							
Skidegate Channel to Rennell Sound							
Shields Bay & south Rennell Sound	135	178	178	LT	2	90	Rodway et al. 1991
West Graham Is. outer waters		375	375	LT	1	76	Vermeer et al. 1983
West Graham Is. Inlets		25	25	LT	1	76	Vermeer et al. 1983
Kindakun Rock to Hippa Island		335	335	LT	1	75	D. Hatler et al. unpubl.
Frederick Is to Langara Is.		150	150	LT	1	75	D. Hatler et al. unpubl.
Parry Passage and Cloak Bay (Langara Island)	50	400	400	Boat counts	20	71	Sealy 1975a

Langara Island (circumnavigation)	20	22	22	LT, all birds visible	2	93	Harfenist 1994
Pillar Bay	145	519	519	Counts from troller	3	83-89	Rodway et al. 1991
Pillar Bay to Masset, excluding inlets	27	54	54	Counts from troller	1	89	Rodway et al. 1991
Virago Sound		168	168	LT	1	90	Rodway et al. 1991
Naden Harbour	0	0	0	LT	1	77	Vermeer et al. 1983
Masset Inlet, Kumdis Island only	41	100	100	LT	3	90	Rodway et al. 1991
Masset Sound & Masset Inlet excluding Kumdis Is.							
Massett Sound to Rose Spit (McIntyre Bay)							
Total for QCI/Haida Gwaii		6063	8538	A total of 9500 is likely, consi	idering i	incomple	ete counts & survey limitations

^{*} Count methods: ST: strip transects; LT: line transects counting all visible birds; GS: grid survey

9.2 Appendix 2. Radar counts of Marbled Murrelets in BC

Appendix 2. Radar counts and population estimates of Marbled Murrelets in May through July. When repeated radar surveys were done, the mean of the annual maximum count per watershed was used.

	Radar	Estimated		
Area	count	population	Notes	Years
SW Vancouver Island				
Clayoquot Sound (Burger 2002)	5536	6000-8000	20 watersheds	1996-98
NW Vancouver Island (Manley 2000)				
Nootka Sound & Esperanza to Tatchu Pt	2012		15 watersheds	1999 & 2001
Tatchu Pt to Kyuquot (Kyuquot Sound)	1572		6 watersheds	1999 & 2001
Checkleset Bay	1011		4 watersheds	1999 & 2001
Brooks Bay	1005		2 watersheds	1999 & 2001
Quatsino Sound	328		4 watersheds	1999 & 2001
Cape Parkins to Cape Scott	2		1 watershed	1999
Total NW Vancouver Island	5930	6500-8000		
Sunshine Coast (Cullen 2002)				
Bute Inlet	623		6 watersheds	2000-2001
Howe Sound & Sechelt Inlet	22		3 watersheds	2000-2001
Jervis Inlet	600		6 watersheds	2000-2001
Toba Inlet and Desolation Sound	1192		6 watersheds	2000-2001
	2437			
Central Mainland (Schroeder et al. 1999))			
Knight Inlet through Kingcome Inlet	930		6 watersheds	1998
Smith Sound and Rivers Inlet	794		5 watersheds	1998
FizHugh Sound	340		2 watersheds	1998
Burke and Dean Channels	514		4 watersheds	1998
Spiller and Mathieson Channels	412		2 watersheds	1998
Princess Royal Channel	365		3 watersheds	1998
Total for Schroeder et al. (1999)	3355	21,352 Sch	nroeder et al.(1999) pi	referred model
		10,000	Likely minimum at 3:	x actual count

·	s, unpublished data)		
Aaltanhash River	25-38	Range of pessimistic	2001
		to optimistic counts	
		given for each	
		watershed by	
Peles lalat	45.50	Steventon and Holmes	0004
Baker Inlet	45-50		2001
Barrie Creek	12-18		2001
Bay of Plenty	20-33		2001
Brim River	36-50		2001
Cedar Creek	24-26		2001
Chambers Creek	26-33		2001
East Inlet	64-72		2001
Gilttoyees Creek	98-107		2001
Green Lagoon	67-73		2001
Kemano River	37-37		2001
Khutze River	57-91		2001
Khutzeymateen	56-181		2001
Kiltuish River	25-43		2001
Kiskosh Creek	7-11		2001
Klekane River	23-27		2001
Kowesas River	41-46		2001
Kwinamass River	44-441		2001
Leverson Creek	110-170		2001
McIsaac River	43-56		2001
McShane Creek	23-27		2001
Toon	99-123		2001
Triumph River	22-31		2001
Union Inlet	29-29		2001
Unknown 1	19-19		2001
Unknown 5	13-27		2001
Total for Northern Mainland	1065-1859		
Total for Northern Mainland			
Extrapolations for total North Coast using		renton, unpubl. data):	

10,128

(90% CL 7,364-12,264)

"Pessimistic" density model

9.3 Appendix 3. Estimating densities using radar counts and GIS

Appendix 3. Estimating densities of Marbled Murrelets in forest habitat using radar counts and GIS data

Reliable estimates of the densities of Marbled Murrelets per hectare of suitable forest habitat would be extremely valuable in management, either for estimating the areas of forest needed for specific populations of murrelets, or conversely for estimating the numbers of murrelets likely to be using a specific area of forest. This analysis uses data from five independent radar studies covering a total of 108 watersheds in BC. Refer to each study for the details in methods, definitions of habitat types and sources of habitat data. Each radar survey site and associated watershed was treated as an independent sample. Fortuitously the five studies had similar numbers of sites (18-26), which simplified comparisons among them.

Clayoquot Sound (CQS) - 18 watersheds were sampled multiple times (usually at least twice per season) over 2-3 years in Clayoquot Sound on the west of Vancouver Island (Burger 2001, 2002).

Northwest Vancouver Island (NWVI) – 21 watersheds were sampled 1-3 times in 1999, and data from other watersheds in which murrelets were not funneled into distinct inland areas were excluded (Manley 2000). This study covered watersheds north of Clayoquot Sound on the west coast of Vancouver Island. In 2001, 13 of these watersheds were sampled again and the mean maximum counts were calculated from the two years, where applicable (I. Manley, unpubl. data).

Sunshine Coast (SC) – Cullen (2002) sampled 21 watersheds on the Sunshine Coast, southern mainland, with most sampled in two years.

Central Coast (CC) – Schroeder et al. (1999) sampled 22 watersheds along the Central Mainland Coast in a single year. The counts made on the Central Coast by Drever and Kaiser (1999) were not used in the analysis because many of the counts were made at inlet mouths or other sites which could not be readily matched with discrete inland areas. Some of the areas covered by Drever and Kaiser (1999) overlapped those sampled by Schroeder et al. (1999).

North Coast (NC) – Preliminary data were included from 26 watersheds on the Northern Mainland Coast sampled in 2001 (Steventon and Holmes 2002).

Counts of Marbled Murrelets

Many sites had been sampled once and others multiple times. Consequently the most consistent measure of murrelet numbers was the maximum count made at each site. Where multiple years had been sampled (Clayoquot Sound, NW Vancouver Island and Sunshine Coast) the mean of each year's maximum count was used. Counts for Clayoquot Sound used here are therefore slightly higher than the mean of the mean annual count used in Burger (2001).

Habitat measures

Measures of available habitat varied across each study, depending on the available GIS information, the type of habitat considered most suitable, and local variations in habitat types. Three measures of habitat were used.

Habitat 1: All mature and old-growth - This category was meant to cover the broadest classifications of mature and old-growth forests given in each study. For Clayoquot Sound, NW Vancouver Island, the Sunshine Coast, and North Coast this was given as all forest over 140 years old (age class 8 and 9) at all elevations, which in reality was mostly >250 years old (age class 9), especially for the two Vancouver Island studies. For the Central Mainland there was no general measure of mature and old-growth in Schroeder et al. (1999), and the broadest habitat category available was the top three categories of the algorithm based on Broad Ecosystem Unit mapping, considered suitable under current conditions (i.e., regenerating logged forests excluded).

Habitat 2: "Most likely habitat" - The second measure of habitat was the habitat found to be most likely to predict suitable murrelet nesting areas in each study. For the two Vancouver Island studies this was low-elevation mature and old-growth below 600 m (Manley 2000, Burger 2001). For the Sunshine Coast this measure was old forest >250 years old with height class >19.5 m in all elevations and reflected measures being applied for habitat selection in the Sunshine Coast (Cullen 2002). For the Central Coast the measure was mature and old-growth, height class 4 (>28.5 m) or higher at all elevations (Schroeder et al. 1999). This measure, based on Forest Cover Mapping information, was preferred to the Broad Ecosystem Unit (BEU) algorithms also used by Schroeder et al. for several reasons: the algorithms down-graded slope habitats now known to be well used by murrelets; forest cover measures are proving more reliable as indicators of habitat than BEU units; and, forest cover measures are most compatible with the measures used in other studies. For the North Coast a Habitat Suitability Index (HSI) was applied to weight the areas of forest in each age and size class (Steventon and Holmes 2002).

Habitat 3: Highest realistic densities - Finally the habitat measures that yielded the highest densities of murrelets, which were also realistic for modeling (covered relatively large portions of the landscape, and found in most watersheds) were considered. For Clayoquot Sound, Northwest Vancouver Island and the Sunshine Coast the categories were the same as Habitat 2 (above). For the Central Coast the top two categories of the algorithm based on Broad Ecosystem Unit mapping, considered suitable under current conditions (Schroeder et al. 1999).

Not surprisingly, Habitats 2 and 3 gave very similar results, but Habitat 2 was probably a more practical and realistic measure of high-quality suitable murrelet habitat. Most of the analysis therefore focused on the first two habitat categories.

Dealing with outliers

The first step in the analysis was to identify and delete obvious outliers, if there were also biological reasons for excluding such outliers. This analysis was done by plotting box-plots

which identified obvious outliers, and by checking all sites which fell outside or on the border of the 5-95% confidence limits for mean density.

For stations which had higher than expected numbers of murrelets, relative to habitat area, a likely cause was that the birds counted at the station were passing from the target watershed into another watershed, thus giving an upwardly biased density. In Clayoquot Sound (Burger 2001, 2002) and NW Vancouver Island (Manley 2000, unpubl. data), the authors had made some adjustments by combining data from a few watersheds where such inter-watershed movements were known or suspected.

There were several possible reasons for excluding stations which yielded fewer than expected murrelets. The most obvious cause, but difficult to confirm, was that many murrelets were passing into the target watershed by some other route and were therefore missed. This was most likely to apply to large watersheds and those with open flat coastlines where there were no constrained flight-paths for the murrelets. A second reason to exclude outliers from very large watersheds was that they might have included habitat which was suitable but simply too far from foraging grounds to be used for nesting. This bias also applied to watersheds at the head of long fjords which were many km from likely foraging grounds.

For example, on the Central Coast densities in the relatively small watershed of Namu (90 birds in a total watershed area of 6835) were many fold higher than most other sites in this area, and the birds might have been passing to other watersheds. At the other extreme, the very large watershed of Kemano River (106,134 ha) on the North Coast yielded only 37 birds and its size and location indicated that much of the watershed was unused by murrelets (D. Steventon pers. comm.). Outliers with higher densities than expected for their study area which were removed included Hesquiat Point (CQS), Malskope (NWVI), Forbes (SC), Namu (CC) and Kwalate (CC). Outliers with exceptionally low densities which were excluded included Rainy (SC), Bella Coola (CC), Kimsquit (CC), Kemano River (NC), Kwinamass (NC), Bay of Plenty (NC), and Barrie Creek (NC). These watersheds are identified in Table A3-1 with asterisks.

Comparison of murrelet densities

Mean densities (murrelets per area of habitat) per study area were calculated as the arithmetic mean of the densities calculated for each watershed (Table A3-2). One-way Analysis of Variance (SPSS 10.0) showed significant differences among the densities in the five study areas for all three of the habitat measures considered. Mean densities from the two west Vancouver Island areas were almost identical, and were significantly higher than those from the other three sites. There were no significant differences among the South, Central and North Coast densities.

To some extent the differences in density reflect differences in the types of forest included as habitat in each study. However, even when the most general habitat measure (Habitat 1) was used for the two west Vancouver Island studies and the "most likely habitat" (Habitat 2) was used for the three mainland studies, the differences in density, although less, were still statistically significant (ANOVA, $F_{4.91} = 6.58$, P < 0.001).

Regional variations in density

Overall, the available data suggest that the west coast of Vancouver Island should be treated separately from the three mainland study areas. Mean densities with the data pooled in this way are shown in Table A3-2.

Application of these preliminary density values requires great care, especially if applied to parts of the province which have not been sampled with radar (i.e., Haida Gwaii/Queen Charlotte Islands and East Vancouver Island). Comparisons of the forest structure, availability of platform limbs, tree size, etc. might indicate whether the habitats are more similar to one or other of the studied areas. More reliable applications of density would be possible if the same measures of suitable habitat could be used to calculate densities across all the study areas and then applied in a similar manner in management use.

Densities derived from very general measures of suitable habitat (e.g., all mature and old-growth) tend to be low. They should be applied only when there are no better measures of habitat, and with the understanding that the habitat so selected will include a portion which is unsuitable for nesting murrelets. If these general low densities are applied to selected high quality habitat they will tend to overestimate the amount of habitat needed. Densities derived from more restrictive or realistic measures of suitability (e.g., Habitat 2 categories using tree age and size classes, and elevation) could be applied when the habitat being selected includes a high proportion that is likely to be suitable for nesting. Continued research is essential to refine the accuracy and application of these density measures.

Table A3-1. Estimates of densities of Marbled Murrelets in forest nesting habitat in British Columbia based on radar counts and GIS habitat measures.

The count of Marbled Murrelets (MaMu) was the mean of the annual maximum count for each survey station.

•					All matur	e and old	d-growth	Mos	t likely h	abitat	Highest	realistic	densities
Study area	Watershed/Survey Station	No. years surveyed	MaMu count (birds)	Total watershed area (ha)	Habitat measure in each study*	Area of forest habitat (ha)	Murrelet density (birds/ha)	Habitat measure in each study*	Area of forest habitat (ha)	Murrelet density (birds/ha)	Habitat measure in each study*	Area of forest habitat (ha)	Murrelet density (birds/ha)
Clayoquot Sound	Atleo	2	118	2732	1	1762	0.067	2	1155	0.102	2	1155	0.102
Clayoquot Sound	Bedwell (excluding Ursus)	3	110	13598	1	8577	0.013	2	2942	0.037	2	2942	0.037
Clayoquot Sound	Boat Basin (Hesquiat)	2	331	5672	1	5250	0.063	2	4574	0.072	2	4574	0.072
Clayoquot Sound	Bulson	3	412	8856	1	7981	0.052	2	3662	0.113	2	3662	0.113
Clayoquot Sound	Clayoquot + 0.5 upper Kennedy	2	494	9432	1	8329	0.059	2	4663	0.106	2	4663	0.106
Clayoquot Sound	Cypre	2	63	5763	1	3523	0.018	2	1769	0.036	2	1769	0.036
Clayoquot Sound	Flores Creek #6	3	120	1742	1	1742	0.069	2	1664	0.072	2	1664	0.072
Clayoquot Sound	Hesq Point Creek **	2	196	1767	1	1752	0.112	2	1570	0.125	2	1570	0.125
Clayoquot Sound	Kennedy (excl. upper valley)	3	334	18769	1	13842	0.024	2	6565	0.051	2	6565	0.051
Clayoquot Sound	Megin (West Megin only)	3	430	10745	1	10321	0.042	2	8189	0.053	2	8189	0.053
Clayoquot Sound	Moyeha	3	596	17930	1	12935	0.046	2	5365	0.111	2	5365	0.111
Clayoquot Sound	Pretty Girl	2	260	3540	1	3362	0.077	2	2706	0.096	2	2706	0.096
Clayoquot Sound	Sydney	2	225	5591	1	5517	0.041	2	3985	0.056	2	3985	0.056
Clayoquot Sound	Tofino Cr + 0.5 upper Kennedy	3	213	6454	1	5232	0.041	2	2624	0.081	2	2624	0.081
Clayoquot Sound	Tranquil	2	268	5870	1	4358	0.061	2	1977	0.135	2	1977	0.135
Clayoquot Sound	Ursus	3	331	7348	1	6367	0.052	2	3032	0.109	2	3032	0.109
Clayoquot Sound	Watta (includes East Megin)	3	650	17341	1	14951	0.043	2	7870	0.083	2	7870	0.083
Clayoquot Sound	Watta South	2	45	1394	1	1394	0.032	2	689	0.065	2	689	0.065
NW Vancouver Island	Amai	1	149	2759	1	2035	0.073	2	1708	0.087	2	1708	0.087
NW Vancouver Island	Artlish	2	570	12453	1	9143	0.062	2	4742	0.120	2	4742	0.120
NW Vancouver Island	Conuma	2	372	12403	1	9714	0.038	2	4367	0.085	2	4367	0.085
NW Vancouver Island	Espinosa	1	115	2743	1	1933	0.059	2	1276	0.090	2	1276	0.090
NW Vancouver Island	Kashutl	1	85	2701	1	1926	0.044	2	1345	0.063	2	1345	0.063
NW Vancouver Island	Kauwinich	2	290	8065	1	5270	0.055	2	3421	0.085	2	3421	0.085
NW Vancouver Island	Klashkish/East	2	1005	9669	1	9219	0.109	2	8610	0.117	2	8610	0.117
NW Vancouver Island	Koprino	1	267	5957	1	3622	0.074	2	2902	0.092	2	2902	0.092
NW Vancouver Island	Leiner	2	294	10504	1	6594	0.045	2	2877	0.102	2	2877	0.102
NW Vancouver Island	Little Zeballos	1	85	4325	1	2391	0.036	2	556	0.153	2	556	0.153
NW Vancouver Island	Malskope **	2	220	3526	1	1996	0.110	2	1251	0.176	2	1251	0.176
NW Vancouver Island	Nasparti	2	177	5890	1	5472	0.032	2	5085	0.035	2	5085	0.035
NW Vancouver Island	Nuchalitz	1	314	4707	1	2986	0.105	2	2739	0.115	2	2739	0.115
NW Vancouver Island	Oukinish	2	160	3824	1	3151	0.051	2	2336	0.068	2	2336	0.068
NW Vancouver Island	Port Eliza	1	28	2573	1	1884	0.015	2	1538	0.018	2	1538	0.018
NW Vancouver Island	Power	2	454	5504	1	4689	0.097	2	3447	0.132	2	3447	0.132
NW Vancouver Island	Sucwoa	1	23	4448	1	2277	0.010	2	847	0.027	2	847	0.027
NW Vancouver Island	Tahsis	2	271	7461	1	4866	0.056	2	2189	0.124	2	2189	0.124
NW Vancouver Island	Tahsish	2	442	23887	1	16239	0.027	2	8009	0.055	2	8009	0.055
NW Vancouver Island	Tlupana/Kleptee	2	236	15667	1	13354	0.018	2	6844	0.034	2	6844	0.034

Table A3-1 continued					All mature	e and old	d-growth	Mos	t likely h	abitat	Highest	realistic (densities
Study area	Watershed/Survey Station	No. years surveyed	MaMu count (birds)	Total watershed area (ha)	Habitat measure in each study*		Murrelet density (birds/ha)	Habitat measure in each study*		Murrelet density (birds/ha)	Habitat measure in each study*	Area of forest habitat (ha)	Murrelet density (birds/ha)
NW Vancouver Island	Zeballos	2	204	19499	1	12373	0.016	2	4178	0.049	2	4178	0.049
Sunshine Coast	Bear (Bute area)	1	93.5	29453	1	5353	0.017	3	3258	0.029	3	3258	0.029
Sunshine Coast	Brem (Toba area)	2	297.5	24598	1	6298	0.047	3	4739	0.063	3	4739	0.063
Sunshine Coast	Brittain (Jervis area)	2	113.0	12223	1	3732	0.030	3	2789	0.041	3	2789	0.041
Sunshine Coast	Dakota (Howe area)	1	8.0	2072	1	1027	0.008	3	853	0.009	3	853	0.009
Sunshine Coast	Deserted (Jervis area)	1	107.0	13523	1	3747	0.029	3	3134	0.034	3	3134	0.034
Sunshine Coast	Forbes (Toba area) **	2	236.0	5612	1	2521	0.094	3	1746	0.135	3	1746	0.135
Sunshine Coast	Homathko (Bute area)	1	103.0	126777	1	16123	0.006	3	9125	0.011	3	9125	0.011
Sunshine Coast	Hunaechin (Jervis area)	1	43.0	15722	1	2473	0.017	3	1515	0.028	3	1515	0.028
Sunshine Coast	McNab (Howe area)	2	7.0	6874	1	1476	0.005	3	478	0.015	3	478	0.015
Sunshine Coast	Orford (Bute area)	2	171.0	42489	1	7157	0.024	3	4796	0.036	3	4796	0.036
Sunshine Coast	Paradise (Bute area)	1	129.0	9007	1	2474	0.052	3	1943	0.066	3	1943	0.066
Sunshine Coast	Powell-Daniels (Toba area)	1	99.0	35745	1	3929	0.025	3	4744	0.021	3	4744	0.021
Sunshine Coast	Quatam (Toba area)	2	200.0	15814	1	5088	0.039	3	4138	0.048	3	4138	0.048
Sunshine Coast	Rainy (Howe area) **	1	7.0	6830	1	2590	0.003	3	2135	0.003	3	2135	0.003
Sunshine Coast	Skwakwa (Jervis area)	1	155.0	20144	1	3939	0.039	3	3189	0.049	3	3189	0.049
Sunshine Coast	Southgate (Bute area)	1	95.0	79871	1	12500	0.008	3	8266	0.011	3	8266	0.011
Sunshine Coast	Tahumming (Toba area)	2	34.0	25571	1	3526	0.010	3	2408	0.014	3	2408	0.014
Sunshine Coast	Teaquahan (Bute area)	1	31.0	15548	1	2175	0.014	3	1611	0.019	3	1611	0.019
Sunshine Coast	Toba (Toba area)	2	325.5	177184	1	26095	0.012	3	19342	0.017	3	19342	0.017
Sunshine Coast	Tzoonie (Jervis area)	2	38.5	16914	1	4047	0.010	3	3117	0.012	3	3117	0.012
Sunshine Coast	Vancouver (Jervis area)	1	143.0	19638	1	7591	0.019	3	5960	0.024	3	5960	0.024
Central Coast	Aaltanhash	1	35	12293	5	5785	0.006	4	2409	0.015	6	3979	0.009
Central Coast	Ahnuhati	1	95	18519	5	6715	0.014	4	1319	0.072	6	3666	0.026
Central Coast	Ahta	1	62	6629	5	5849	0.011	4	3061	0.020	6	2708	0.023
Central Coast	Bella Coola **	1	13	144796	5	15368	0.001	4	15325	0.001	6	6157	0.002
Central Coast	Chuckwalla/Kilbella	1	462	71610	5	21357	0.022	4	13673	0.034	6	10442	0.044
Central Coast	Draney	1	31	11089	5	9793	0.003	4	4550	0.007	6	4351	0.007
Central Coast	Ellerslie Lake	1	312	21083	5	8266	0.038	4	6127	0.051	6	5059	0.062
Central Coast	Green	1	197	19123	5	7981	0.025	4	4661	0.042	6	5418	0.036
Central Coast	James Bay	1	100	4339	5	3941	0.025	4	1804	0.055	6	1919	0.052
Central Coast	Johnstone St. A/B	1	77	13000	5	4215	0.018	4	4731	0.016	6	4214	0.018
Central Coast	Kakweiken	1	297	32370	5	15374	0.019	4	8060	0.037	6	4834	0.061
Central Coast	Khutze	1	133	27678	5	6197	0.021	4	3319	0.040	6	1601	0.083
Central Coast	Kimsquit **	1	17	101714	5	17071	0.001	4	14607	0.001	6	0	-
Central Coast	Koeye	1	250	17349	5	6790	0.037	4	8857	0.028	6	6017	0.042
Central Coast	Kwalate **	1	195	9317	5	0	-	4	725	0.269	6	0	-
Central Coast	Kwatna	1	392	37758	5	14878	0.026	4	6853	0.057	6	5955	0.066
Central Coast	Namu **	1	90	6835	5	251	0.359	4	4310	0.021	6	251	0.359
Central Coast	Nekite	1	55	41000	5	15307	0.004	4	6557	0.008	6	6332	0.009

Table A3-1 continued				All mature and old-growth				Most likely habitat			Highest realistic densities		
Study area	Watershed/Survey Station	No. years surveyed	MaMu count (birds)	Total watershed area (ha)	Habitat measure in each study*		Murrelet density (birds/ha)	Habitat measure in each study*		Murrelet density (birds/ha)	Habitat measure in each study*	Area of forest habitat (ha)	Murrelet density (birds/ha)
Central Coast	Sim	1	31	30405	5	5174	0.006	4	321	0.097	6	209	0.148
Central Coast	Skowquiltz	1	92	27296	5	0	-	4	3248	0.028	6	0	-
Central Coast	Wakeman	1	250	68919	5	26518	0.009	4	15330	0.016	6	10173	0.025
Central Coast	Wannock	1	169	85018	5	25081	0.007	4	20028	0.008	6	14387	0.012
North Coast	Aaltanhash_River	1	25	12301	1	2784	0.009	7	2427	0.010	4	1457	0.017
North Coast	Baker_Inlet	1	45	2075	1	1001	0.045	7	1015	0.044	4	485	0.093
North Coast	Barrie_Creek **	1	12	10850	1	1840	0.007	7	1467	0.008	4	1205	0.010
North Coast	Bay_of_Plenty **	1	20	7461	1	6453	0.003	7	2831	0.007	4	1359	0.015
North Coast	Brim_River	1	36	26616	1	3054	0.012	7	2864	0.013	4	1824	0.020
North Coast	Cedar_Creek	1	24	2407	1	893	0.027	7	1227	0.020	4	801	0.030
North Coast	Chambers_Creek	1	26	8911	1	5176	0.005	7	4221	0.006	4	2187	0.012
North Coast	East_Inlet	1	64	3152	1	1582	0.040	7	1284	0.050	4	650	0.099
North Coast	Gilttoyees_Creek	1	98	28512	1	3797	0.026	7	3510	0.028	4	2396	0.041
North Coast	Green_Lagoon	1	67	14143	1	5075	0.013	7	5074	0.013	4	3081	0.022
North Coast	Kemano_River **	1	37	106134	1	11057	0.003	7	12800	0.003	4	11861	0.003
North Coast	Khutze_River	1	57	20734	1	3568	0.016	7	3068	0.019	4	2169	0.026
North Coast	Khutzeymateen_River	1	56	42196	1	9968	0.006	7	9523	0.006	4	6083	0.009
North Coast	Kiltuish_River	1	25	13920	1	2190	0.011	7	2045	0.012	4	1211	0.021
North Coast	Kiskosh_Creek	1	7	3094	1	1230	0.006	7	696	0.010	4	212	0.033
North Coast	Klekane_River	1	23	8022	1	2204	0.010	7	1667	0.014	4	924	0.025
North Coast	Kowesas_River	1	41	37409	1	9063	0.005	7	5174	0.008	4	3032	0.014
North Coast	Kwinamass_River **	1	44	33345	1	14236	0.003	7	11396	0.004	4	6598	0.007
North Coast	Leverson_Creek_A	1	110	9012	1	4451	0.025	7	2600	0.042	4	766	0.144
North Coast	McIsaac_River	1	43	3508	1	1468	0.029	7	1096	0.039	4	689	0.062
North Coast	McShane_Creek	1	23	3573	1	1064	0.022	7	860	0.027	4	439	0.052
North Coast	Toon_River_Estuary	1	99	13104	1	3715	0.027	7	3122	0.032	4	1853	0.053
North Coast	Triumph_River	1	22	8609	1	2883	0.008	7	2118	0.010	4	1348	0.016
North Coast	Union_Inlet	1	29	6738	1	2725	0.011	7	2003	0.014	4	914	0.032
North Coast	Unknown_1	1	19	1223	1	404	0.047	7	380	0.050	4	228	0.084
North Coast	Unknown_5	1	13	2568	1	1282	0.010	7	1095	0.012	4	619	0.021

^{*} Habitat measures used in this analysis

^{1 =} all mature and old-growth (age class 8 and 9; >140 years old), all elevations

^{2 =} mature and old-growth below 600 m

^{3 =} old growth (age class 9, > 250 years old), height class 3 (>19.5 m) or higher

 $^{4 = \}text{mature}$ and old growth (class 8 and 9; >140 years old), height class 4 (>28.5 m) or higher

^{5 =} top 3 habitat categories using Broad Ecosystem Unit classification (see Schroeder et al. 1999).

^{6 =} top 2 habitat categories using Broad Ecosystem Unit classification (see Schroeder et al. 1999).

^{7 =} Habitat Suitability Index (HSI) weighted area (see Steventon and Holmes 2002)

^{**} These watersheds were considered outliers within their study areas and were excluded from some analyses.

Table A3-2. Mean ± SD densities of Marbled Murrelets (birds per ha) in the five study areas in BC, calculated with three different measures of suitable habitat. The results of ANOVA tests for each habitat measure are given. Tukey post-hoc tests were used to identify significant differences among study areas: areas with different letter codes (a,b,c) are significantly different, those with the same letter are not significantly different.

		Habitat 1 (all mature & old growth)	Habitat 2 ("most likely habitat")	Habitat 3 (highest realistic densities)
Study areas	N	Mean ± SD	Mean ± SD	Mean ± SD
Clayoquot Sound	17	0.047 ± 0.018 a	0.081 ± 0.029 a	0.081 ± 0.029 a
NW Vancouver Is	20	0.051 ± 0.029 a	0.083 ± 0.038 a	0.083 ± 0.038 a
Sunshine Coast	19	0.022 ± 0.014 b	0.029 ± 0.018 b	0.029 ± 0.018 b
Central Coast	17	0.017 ± 0.011 b	0.035 ± 0.024 b	0.043 ± 0.036 b
North Coast	22	0.019 ± 0.013 b	0.022 ± 0.015 b	0.042 ± 0.035 b
ANOVA		F4,90 = 15.15, P<0.001	F4,91 = 25.06, P<0.001	F4,90 = 11.25, P<0.001
West Vancouver Island	37	0.049 ± 0.025	0.082 ± 0.034	0.082 ± 0.034
BC Mainland	58	0.019 ± 0.013	0.028 ± 0.019	0.034 ± 0.023
ANOVA		F1,93 = 61.04, P<0.001	F1,94 = 97.89, P<0.001	F1,93 = 65.87, P<0.001
All areas pooled	95	0.031 ± 0.023	0.049 ± 0.037	0.055 ± 0.038

Notes: Outliers were excluded from this analysis (see text). Sample size (N) is number of watersheds per study. One watershed in the Central Coast had no areas of Habitat 1 or 3 and was excluded for those categories. West Vancouver Island includes Clayoquot Sound and NW Vancouver Island; BC Mainland includes the other three study areas.

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